CARNIVOROUS PLANT NEWSLETTER

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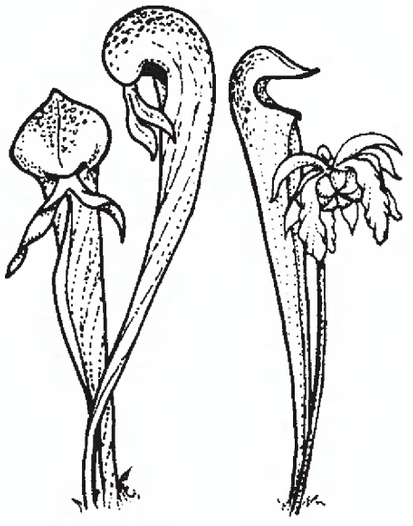

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Front Cover: Plants of a 'paddle-leaf' form of *Drosera capensis* regrowing after winter dormancy at the top of the Gydo Pass. Photo by Robert Gibson. Article on page 173.

Back Cover: *Nepenthes mapuluensis* illustration by François Sockhom Mey. Article on page 148.

Carnivorous Plant Newsletter is dedicated to spreading knowledge and news related to carnivorous plants. Reader contributions are essential for this mission to be successful. Do not hesitate to contact the editors with information about your plants, conservation projects, field trips, or noteworthy events. Advertisers should contact the editors. Views expressed in this publication are those of the authors, not the editorial staff.

All correspondence regarding dues, address changes and missing issues should be sent to the Membership Coordinator at the ICPS. Do not send such correspondence to the editors. Checks for subscriptions should be made to the International Carnivorous Plant Society in US funds. Dues, including a subscription, are $30 per year.

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Membership Dues Increase

Starting January 1, 2021, the dues for a one-year membership will increase to $35. The price of library subscriptions and multiyear memberships will not change.

Board changes

The ICPS Board recently made the following changes to its director portfolios and welcomed a new Director. Brent Jones, took on a new portfolio to focus on growing international membership and conferences. Carson Trexler joined the board as the Director for Conservation and Research.

Carson has been a member of the ICPS since 2007. His relationship with CPs focuses on the ornamental horticulture of *Sarracenia*. Carson has worked at Sarracenia Northwest, a Carnivorous Plant nursery, for 3 years, and attends Oregon State University, pursuing a degree in Horticulture. He lives in Portland, Oregon, USA, where he enjoys being an active part of the local CP community. Carson is ambitious to develop this portfolio into an effective, modern office for the purpose of CP research and public awareness about conservation. In particular, he is keen to engage the ICPS membership, by showcasing our work through CPN and other outlets. Carson will focus on expanding the ICPS's involvement in conservation projects in the United States and Internationally, and working closely with existing conservation involvements.

Carson Trexler.

From the jungle back to the drawing board...and back: An interview with François Sockhom Mey

Marcel van den Broek • marcel@carnivorousplants.org

In a time that we can't travel as we would wish; you can't just walk off into the field and have a great fieldtrip to report. Travelling within Europe is hard enough these viral days. I had hoped to see my good friend François in Ghent at the European meeting, but unfortunately that annual institute of carnivorous plant fun also got killed by COVID-19. What follows is a properly social distanced, interview with François Sockhom Mey.

Marcel: Most people in the CP community connect you with the rediscovery of *Nepenthes thorelii* and the discovery of *Nepenthes bokorensis*, but you also make beautiful CP illustrations. How long have you been drawing and what subjects do you draw?

François: That may sound a cliché, but I've been drawing as long as I can remember. Drawing plants is relatively recent though. As a child, I mainly drew characters, animals, portraits sometimes. Very quickly, I turned my interest into comic book drawing, a field I have investigated for more than 25 years. For what seemed to be an endless time, I tried to finish and publish a graphic novel. In vain. In fact, I had eventually found a publisher and my work was scheduled to be released when I abruptly realized that I would not be mentally able to terminate that project. The gestation had taken way too much time and the baby was born dead. I was feeling unable to properly achieve the book. The resentment was vivid, and I needed to move on to something else. All of a sudden, I quit drawing comic books, a very painful decision so to speak. That was in late 2017.

I had another passion then: carnivorous plants. My interest for it really started in 2004 although I had a general interest in plants before that: I used to rear various species of caterpillars and others insects when I was a child and had a basic knowledge in botany.

In 2009, many years before I abandoned my graphic novel project, I published my first scientific botanical illustration with the description of the Cambodian and endemic pitcher plant species *Nepenthes bokorensis*. It was the very first *Nepenthes* species I described as a publishing taxonomist. As a non-academic, I had taught myself how to write and publish a scientific description (and been largely guided in the process by a few experts that have now become longtime friends). While I was preparing that first scientific work, it was clear to me that I would find a way to produce the botanical illustration myself although it was also obvious that doing a botanical plate had little to do with composing a comic book strip. I was confident that I could make it though and, in my mind, I potentially had the skills and the incentive: I didn't want the process of doing a botanical illustration to be as painful as it was at the time for the creation of my comic book.

Therefore, in the same way that I had studied taxonomy, I spent countless hours and nights understanding the field of botanical illustration. The *Nepenthes* drawings published in Benedictus Danser's monograph (1928) and Jebb & Cheek's (1997, 2001) were particularly useful in my schooling as well as various volumes of the Flora of Cambodia, Laos and Vietnam that include many drawings of non-carnivorous plants. Oddly, in that period, I didn't research any of the contemporary botanical illustrations and illustrators. I worked as a hermit, lost in decades and centuries old botanical plates, completely unaware of the productions of my contemporary colleagues.

When I provided that first illustration, I deemed the exercise as an interesting and an enjoyable recreation, but I didn't think I would investigate botanical illustration much further. It was more

like a side interest that I would practice occasionally when needed. I was too obsessed then with my grand graphic novel. I remember I had to produce the *N. bokorensis* illustration in a hurry. There was a competitor paper at the time and I suddenly realized that I would have no time to further study the art of botanical illustration: I had to literally produce the illustration overnight, from scratch, if I wanted to publish first. That weekend, in March or February 2009, I found out I had no proper drawing paper and I used a mere office sheet for printer! My paper eventually came out first along with that first clumsy botanical plate. Little did I realize at the time that this illustration would be the first of an ongoing series.

Marcel: So, you are a self-taught artist?

François: I'm a completely self-taught illustrator. I have a degree in modern literature and am a certified teacher for middle school and high school, but never took proper classes for drawing and painting although, obviously, I have studied and am still studying the discipline. The same thing applies for botany and taxonomy. Although I authored and co-authored a number of botanical papers, I am academically trained in literature only. Retrospectively, I think I would have loved to take classes in both fields, it would have saved me some time, but at the end I am happy with the path I've chosen. In the future, if given the chance I think I will take classes to improve, especially in the art of botanical illustration.

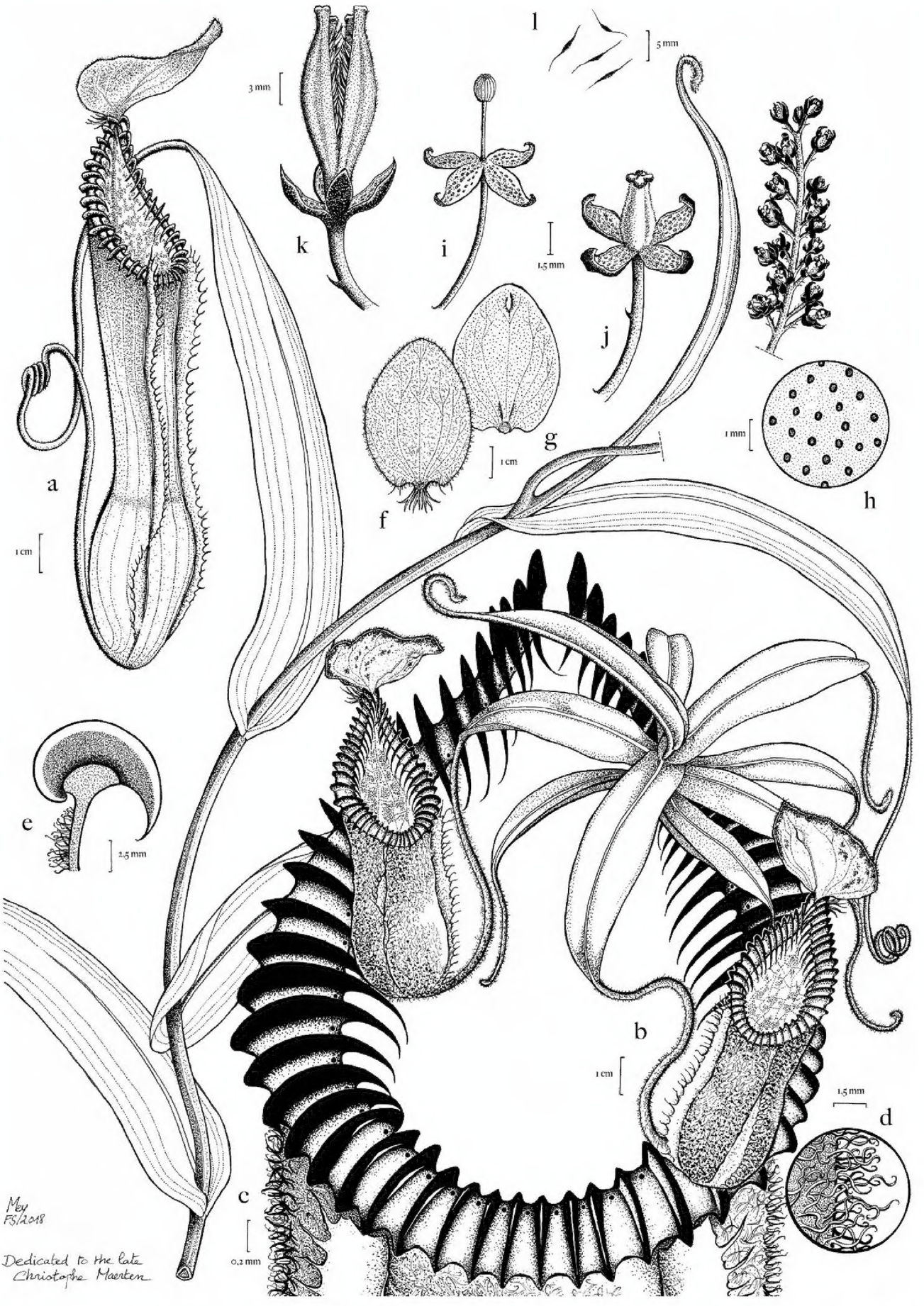
Marcel: That *N. bokorensis* drawing was followed by many illustrations for scientific papers and books. Can you name some of your work?

François: In 2009, when I just drew that *N. bokorensis* illustration, I was asked by Stewart McPherson (whom I made the acquaintance with about 2 years before) to publish several diagrams showing leaf and pitcher morphology for his forthcoming Pitcher Plants of the Old World, Volume Two, a monograph on *Nepenthes* and *Cephalotus*, that would be published by Redfern Natural History. Stewart subsequently asked for more commissions for other Redfern titles the following year.

2010 would turn out to be a very productive year for my standards as I illustrated 5 *Nepenthes* for academic papers: another Cambodian endemic, *Nepenthes holdenii*; the elusive Vietnamese *N. thorelii* based on herbarium material only as there was no available picture of that species at the time; as well as three Filipino species: *Nepenthes palawanensis*, *N hamiguitanensis*, and *N. gantungensis*. On top of this, I produced a series of plates for Redfern Natural History to showcase various genera of carnivorous plants. These were interesting work to do as I got to investigate botanical illustration much further and got to draw many different types of plants, from the well-known *Drosera* and *Pinguicula* to the more obscure (to the general public) *Ibicella*, *Roridula*, and *Triphyophyllum*.

The following years, I would produce further similar work (pencil illustrations mainly): *Nepenthes* illustrations included in taxonomical descriptions of new species (*N. nigra*, *N. pantaronensis*, *N. talaandig*, *N. amabilis* (now *N. sumagaya*), *N. justinae*), various color sketches of *Sarracenia* and *Darlingtonia* for Redfern's Sarraceniaceae of North America monograph, as well as a short series of inked botanical plates for Redfern again: two *Utricularia* plates (one showing *Utricularia intermedia* and the other highlighting bladderwort trap mechanism), *Drosera anglica* and *Pinguicula vulgaris*. These last four were published in Carnivorous Plants of Britain and Ireland.

In 2016, I was commissioned to produce a plate showing *Pinguicula gypsicola* and *P. lusitanica* as well as a *Pinguicula mesophytica* watercolor for Redfern's two-volume monographs on the genus *Pinguicula*. Currently, my last scientific illustration is a botanical plate for a new *Nepenthes* species



Nepenthes diabolica A.Bianchi, Chi.C.Lee., Golos, Mey, M.Mansur & A.S.Rob. (formerly "Red Hamata Hairy").

from Sulawesi (*Nepenthes diabolica* A.Bianchi, Chi.C.Lee., Golos, Mey, M.Mansur & A.S.Rob.) known informally in horticultural circles, since 2004, under the name *Nepenthes* "Red Hamata Hairy". I started this illustration in late 2018 and finished it more than one year later. I was delighted to have it 'Highly Commended' in the 2020 Margaret Flockton Award contest for my first participation. I reckon overall that that is not a lot of work for more than a decade of activity, but like I said, botanical illustration was until recently only a side interest. I was working at the time on a graphic novel of nearly 200 pages on top of the commitments of a full-time job as a teacher.

Marcel: On Facebook and Instagram you show your work in progress in your A Garden's Chronicle. How many hours does an average drawing take?

François: It depends on the type of illustration. Lately, I was commissioned for a *Sarracenia* natural hybrid watercolor that required about 30 hours. I am currently working on a large *Nepenthes clipeata* watercolor that will likely exceed the 60 hours mark. I am slow unfortunately. The fact is I like to take pauses, listen to new music, browsing books, watering and talking to my plants, get distracted… I guess I could do a fine illustration in a few hours, but then I would see too many flaws. That being said, I still do see tons of flaws even after 60 hours spent on a piece. Actually, most of the time, flaws, as well as my own limits, are all I can see at the end of a piece. But luckily for me some people get enthusiastic with my work and then I feel much better.

Marcel: What is the most difficult part of a carnivorous plant to draw?

François: For me? Intricate foliage. *Drosera magnifica* and *Drosophyllum lusitanicum* were mini nightmares to draw. Sundew and the likes are often very two-dimensional so it's hard to make them alive in the paper and I guess I sometimes lack the patience to work on some important details that would improve the whole illustration and I unfortunately rush a bit. I am correcting this poor attitude in my current works. I know I also need to improve the light rendition of the dewy species mucilage, but it's hard to succeed without using a dark background, something I was not interested in doing so far. I will probably do it eventually for the next sundew pieces. I am very impressed when I see detailed drawings or paintings of plants with complex foliage. Look at how Rogério Lupo handled *Drosera magnifica* or Sansanee Deekrajang's recent rendition of *Pinus sylvestris*. Breathtaking.

Marcel: Much of your latest art shows species in their habitat which is a totally different style from the more technical botanical illustrations for scientific papers. Do you prefer either style?

François: I stuck to pencil and black and white botanical illustration for years, but in 2016 I was commissioned to do that watercolor painting for Redfern's two-volume *Pinguicula* monograph. On that occasion, I imagined a scene where the Central American *Pinguicula mesophytica* would be pollinated by the hummingbird *Lampornis vidiripallens*. That was the first time I would depart a bit from science. While the depiction of the plant and the bird were scientifically correct, there was no recorded proof that the hummingbird was one of the carnivorous plant pollinators. It was just a possibility as they occur in the same region. For the first time, I let imagination slip into one of my botanical works. Imagination and phantasmagoria were things that I tried to smother in my botanical work while they were free flowing in my graphic novel project.When I quit drawing the comic book in late 2017, I was not able to hold a pencil or a brush for months, for almost the next 2 years in fact. At the beginning of 2018, my life got into drastic changes on a personal level and the year and

Drosera cistiflora.

a half that would follow was a long process of not only building myself back as a person, but also as an artist. The botanical plate of *Nepenthes* "Red Hamata Hairy" was the unique drawing I would complete in these 2 years. A faint spark in a desert of white endless sheets. I felt no pleasure nor joy doing it; I saw it more like a way of keeping myself more or less alive as an artist. Eventually, as I was feeling better and in peace, I longed to draw again. Not comic books, as I finally understood

this was not my path and that I had to move onto something else. I had realized (although I suspected that well before that time, but was then far from ready to accept the idea) that all these years, what I deemed secondary –botanical illustration– was making me happy while comic book –that I thought was essential to me– was profoundly hurting me, because of the inner nature of the personal story I was trying to convey. Thus, I decided to give botanical illustration a chance. However, I couldn't resign myself to the classical botanical plate showing an isolated plant on a white background. The need of telling a story, creating an atmosphere was still strong and so in November 2019, I drew the discovery of *Nepenthes pervillei* by the French horticulturist Auguste Pervillé. This imaginary scene depicts in a quite dramatic way the moment Pervillé would discover the Seychelles pitcher plant, an unknown species to science at the time. It is not difficult to detect the comic book influence in that piece. Similarly, I would try to create a kind of atmosphere in the following works: *Drosera magnifica*, *Heliamphora macdonaldae*, *Utricularia delphinioides*, *Cephalotus follicularis*, *Sarracenia leucophylla*. Although these paintings are merely a few months old, I have mixed feelings about them; they are more like transition works. However, the comic book experience taught me that it is now mandatory for me to finish what I'm undertaking whether I am happy or not with it.

After this first series of habitat watercolors, I decided to try a more classical approach with my versions of *Drosophyllum lusitanicum*, *Nepenthes epiphytica*, and *N. mapuluensis*. I draw satisfaction from both style of illustrations, I like the codes of the classical botanical plate where one tried to express as much as possible in a delimitated relatively narrow frame and with a set of rules. I see it like writing a sonnet in poetry (sorry, that's the French literature teacher waking up) while drawing and painting a plant in habitat require other skills. As a matter of fact, illustrating a plant in habitat is also a tradition in botanical illustration albeit arguably less popular than the classical plate with isolated plant. My approach to the habitat painting might be a bit different than the tradition though, as I do not only want to depict the plant's environment, but also want to create an atmosphere and to suggest some feelings. These days, I am starting a series of paintings that will see me favor this approach: an accurate depiction of plants with a personal vision, the expression of the feelings that overwhelmed me when I saw the plants in habitat or what I felt when I imagined them while reading about their habitat.

So, no favored style really, but rather a quest for exploration. I am planning to do several short series of illustrations in the next months: group of species gathered in vintage posters with captions; plants growing in dramatic cliff; carnivorous plants lurking in mossy forest with a fantastic and eerie atmosphere and more classical black and white botanical plates. I am also on the verge of starting non strictly botanical illustrations: paintings inspired by nature, plants, and (personal) tales. I guess my need of telling a story is coming back in some way.

Marcel: If you could only make just one more drawing, which species would it be?

Francois: Very likely, the man-eating tree from Madagascar. Or –hoping not sounding too ambitious or arrogant– the definitive Venus Fly Trap illustration, the one painting or drawing people would immediately refer to when looking for an image of this iconic species.

Marcel: So, not so long ago you started selling your drawings, what made you decide to do that?

François: Two different reasons: making peace with drawing, with art, as a whole, as it used to be very painful for a long time and funding new botanical trips as a researcher. Despite these troubled times, there's still much to discover and I want to get lost in the wild again. Bar two expeditions, all

Nepenthes pervillei.

Cephalotus follicularis.

my past botanical trips have been covered at my own expense. It seems to me that selling botanical illustrations is quite an elegant way to fund botanical trips that will result in documenting rare species or discovering new ones.

Marcel: Besides drawings you now offer stickers and bookmarks, how did you come to add those to your repertoire?

François: That's part of my modern adventure. Starting to sell prints and drawings helped me to connect with people (you need to when you create, advertise, and sell) to be less reclusive like I was when I was comic-book drawing (although I used to go out and give CP lectures on a regular basis). I found out that bookmarks and stickers are quite sought after. Hence, I decided to produce a few. I see them as a way to expand my offer and to achieve my goal faster: funding botanical expeditions, immersing myself into Nature again, documenting plants as a taxonomist and a botanical illustrator, and coming back before leaving again. This is a loop I thrive to get lost into until the end.

Marcel: So, I'm curious. Can we expect other products featuring your art too? Say, fridge magnets, coffee mugs?

François: Vintage posters with groups of species and captions are scheduled as I mentioned. For examples, I am toying with the idea of making a *Nepenthes* of Mount Kinabalu poster, one with the *Sarracenia flava* varieties, two with all the *Heliamphora* species, and maybe one with the now four Queensland sisters. Maybe a calendar. An art book certainly. I have considered fridge magnets and mugs and they might be available, likely in very limited quantities, but I am still hesitating as I mainly want to stick with stationery items that I can produce from scratch in my studio.

Marcel: Every field has great names and there are many botanical artists. Do you have anyone who you really admire for their style and/or skill?

François: That's such a vast question. When I started to sell prints, I got advice from my three teenage children to use social media actively to promote my work. I created a web shop on Etsy (always under the guidance of my children, especially my eldest daughter); I started to use my Facebook and Instagram accounts, first created to promote my natural history blog ("A Garden's Chronicle"), to now highlight my botanical illustrations. Thanks to Facebook and Instagram algorithms, I found out, these last 8 months, about the existence of my peers. It was a real shock.

I didn't suspect the world of botanical illustration to be so creative and diverse. I was overwhelmed and spent nights in awe. There were talents everywhere, so many gifted people and awe-inspiring art. I had spent years investigating the art of comic book, but was completely ignorant of what was going on in botanical illustration. I was turned upside down when I was confronting to this whole new universe.

These days, I am always looking forward to seeing the new posts or work of great illustrators such as Claire Felloni, Lucy Smith, Deborah Lambkin, Anna Voystekhovitch, Esmée Winkels, Rogério Lupo, Marney Ward, Eunike Nugroho, Jessica Shepherd, Ingrid Elias, or Anna Mason, but there are many many more that I could mention. Closer to me, I have a lot of respect for my botanist friend Alastair Robinson who has started illustrating plants more or less at the same time as me and has improved tremendously over the years. As a general rule, I favor artists who have a clear signature and style, that I can recognize almost immediately, who clearly propose their personal rendition

Sarracenia leucophylla.

of a plant; people who don't compromise on the accuracy of science and at the same time try not to simply copy a photograph. Don't get me wrong, painting using a couple of pictures as references and making your piece looking like a photo obviously requires a blatant talent (that I don't have), but that is a prowess that leaves me completely unmoved. Equally as admirable and appealing to me, maybe more, are the beautifully strange creations of illustrators inspired by plants and nature in general such as Fay Helfer, Stephanie Law, Florence Legendre, Stéphanie Ledoux (although she's mainly doing portraits), or Lauren Marx. They're creating paths I want to explore as well while making my own.

All these artists –almost all women– are inspiring and challenging. They keep me invigorated and I now need my daily fix of their wizardry. Not to mention that many of them turned out to be exquisite people to interact with.

MARCEL: Thank you François and I hope you will be back in the field soon, but please do continue to use your drawings as means of funding as many people love them.

For those who haven't found François' great and very reasonably priced work, which I highly recommend: He has a shop hosted by Etsy: https://www.etsy.com/fr/shop/Agardenschronicle

On the regulation of dissolved oxygen by *Nepenthes* pitchers

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Keywords: *Nepenthes*, pitcher plants, dissolved oxygen levels, pitcher fluid regulation, phytotelmata.

Abstract: The digestive fluid of tropical pitcher plants (Nepenthaceae: *Nepenthes* L.) typically harbor communities of symbiotic organisms in nature, an example of a phytotelm ecosystem. While the inhabitants of pitchers (primarily the arthropods) have been described and studied from a community ecology perspective for over a century, many abiotic properties of the fluid environment have not been thoroughly documented. As the abiotic properties of the pitcher fluid micro-environment may have fitness and/or functional consequences on the inhabitants, it is of interest to examine intra- and interspecific variation in fluid properties. Here I report observations of dissolved oxygen levels in *Nepenthes* pitchers. I find evidence that *Nepenthes* pitchers actively modify dissolved oxygen levels in the fluid and that this oxygenation ability may vary ontogenetically, with relatively hypoxic conditions in newly opened pitchers and high oxygen levels maintained in more mature pitchers.

Introduction

Most phytotelmata (plant-held aquatic microhabitats) are ephemeral resources prone to desiccation and hypoxia (Kitching 2001). Communities of heterotrophic organisms living within water-filled tree holes or bromeliad tanks, for example, can easily deplete the oxygen dissolved in the water unless photosynthetic algae are also present, as the host plant tissues lack the ability to actively maintain the dissolved oxygen (DO) of their phytotelm (Laessle 1961). Pitcher plants, on the other hand, can actively maintain DO. Past studies demonstrated that *Sarracenia* pitchers normally maintain high DO even with communities dominated by heterotrophic inquilines (Cameron *et al.* 1977; Bradshaw 1983). *Sarracenia* pitchers contain chloroplasts in the epidermal cells of the pitcher interior, which is unusual as this is non-stomatal tissue that would typically lack chloroplasts in terrestrial plant species (Joel & Gepstein 1985). Bradshaw (1983) demonstrated that *Sarracenia* (Sarraceniaceae) pitchers assimilate dissolved CO_2 in the presence of light while maintaining stable DO without much regard to light. The oxygenation of pitcher fluid by the host plant allows the survival of the highly oxygen-sensitive *Metriocnemus knabi* (Cameron *et al.* 1977), an obligately associated chironomid midge, which benefits the host *Sarracenia purpurea* by aiding in prey digestion (Heard 1994). Thus, fluid oxygenation seems to have an important role in enabling this mutualistic association. On the other hand, dissolved oxygen levels in the pitchers of the convergently evolved Old World tropical pitcher plants (Nepenthaceae: *Nepenthes*) have not been described in published reports, to my knowledge. Studies on the photosynthetic efficiency of *Nepenthes* pitchers and laminae for four species (*N. talangensis*, *N. alata*, *N. mirabilis*, and *N. ventricosa*) showed that pitchers exhibit relatively low net assimilation rates (Pavlovič *et al.* 2007, 2009; Adamec 2010). That the functions of digestion and photosynthesis are carried out by two distinct organs in *Nepenthes* as opposed to the dual role of the pitchers of the Sarraceniaceae presents an interesting complication when trying to draw parallels between what was shown for *Sarracenia* and what may be the case in

Nepenthes. Relative to *Sarracenia*, *Nepenthes* pitchers do not have as much photosynthetic tissue, but there are increased chloroplasts in the digestive zone, surrounding the glands (Pavlovič *et al.* 2007). Thus, I sought to determine whether *Nepenthes* pitchers oxygenate their fluid as has been shown for *Sarracenia*. I was interested in whether there might be species and/or ontogenetic differences in pitcher fluid oxygenation. Here I present my observations of oxygen levels in *Nepenthes* pitchers from various natural and experimental contexts.

Materials and Methods

In July-September 2013, I conducted exploratory investigations of oxygenation in *Nepenthes* using 3 small potted individuals each of *N. maxima*, *N. albomarginata*, and *N. ampullaria* (Black Jungle Terrarium Supply), reared in a growth chamber in Cambridge, Massachusetts (12 hour day/night cycle, 80% relative humidity, 30°C). To examine whether pitchers can manipulate oxygen levels in the absence of inquiline communities, I added distilled deionized water (ddH_2O) to pitchers which I had emptied and washed out (removing any prey items). Drawing up 1 mL water samples into a Luer-Lok syringe, carefully so as to prevent agitation and aeration of the sample, I then measured DO concentration in the samples using the Shriwastav *et al.* (2010) micro-Winkler titration method (110 samples). The Shriwastav *et al.* (2010) method is a modification of a standard technique for measuring DO in limnological studies, which was adapted for measuring small samples. The sample is kept under a layer of n-hexane before fixing in order to prevent atmospheric O_2 contamination. The sample is fixed with 5 µL each of $MnSO_4$ and alkali-azide-iodate solution; next the resulting precipitate is dissolved with 0.1 mL H_2SO_4, and then finally the resulting iodine solution is stained with starch indicator and titrated with sodium thiosulfate until clear. I also measured oxygen levels from ddH_2O in glass containers with this method (22 samples) and also measured DO in the endogenous fluid from pitchers that had just opened one or two days prior (7 samples). For the majority of measurements in this experiment, I collected and fixed the sample for titration within 24 hours of adding the ddH_2O, but in a few cases I measured DO in pitchers/glass containers after letting the ddH_2O sit for ~1 week (10 samples, including 2 from glass containers) or ~1 month (14 samples, 3 from glass) after its addition. For statistical analysis, I conducted linear mixed models in R 3.5.0 (RCoreTeam 2013) using the 'lmer' function in the 'lme4' package (Bates *et al.* 2015) and including plant/pitcher ID as a random effect to account for multiple sampling and correct for pseudoreplication.

In January 2014, I took opportunistic measurements of dissolved oxygen levels in unopened pitchers of wild *Nepenthes gracilis* in Kent Ridge Park, Singapore using the Shriwastav *et al.* (2010) micro-Winkler titration method. I sampled fluid from 10 unopened pitchers, but as many of these had fluid volumes less than 1 mL, I had to pool them, which resulted in 5 samples for titration.

In August 2014, I measured dissolved oxygen concentrations in *Nepenthes* pitchers in a Singapore horticultural glasshouse (HortPark *Nepenthes* nursery; plants sourced from Borneo Exotics Ltd.) with a well-regulated indoor environment (16°C temperature, 80% relative humidity). I used a fiber-optic probe and spectrometer-based sensing system (Ocean Optics, Inc., Dunedin, Florida, USA). The probe was calibrated on-site using saturated and deoxygenated ddH_2O standards. Pitchers were covered with a dark opaque fabric during measurements to mitigate noisy measurements that could occur due to ambient light. I recorded point measurements taken from the middle of the fluid column; I made sure to keep the probe in the same relative position for each measurement as I had observed possible differences in oxygen level depending on the depth of the probe within individual pitchers.

In February 2016, I collected fluid from several wild *N. gracilis* in Kent Ridge Park in Singapore, homogenized and filtered that fluid in a sterile bottle-top vacuum filter, and added 1.0 mL allotments of this stock fluid to open glass vials (with similar dimensions to *N. gracilis* pitchers) and healthy mature pitchers from potted *N. gracilis* plants that I had emptied out and washed beforehand. Each vial or pitcher also received an equal-sized mealworm segment and each container type was equally divided into four treatments: one mosquito (Diptera: Culicidae, either *Culex* or *Tripteroides*) larva added, one *Endonepenthia* (Diptera: Phoridae) larva added, a combination of one mosquito and one *Endonepenthia* larva added, and no larvae added. I measured oxygen levels with an oxygen optrode (Ocean Optics) after about 18 hours. This experiment was conducted in a greenhouse at the Raffles Institution, with the original goal of observing the effects of inquilines on pitcher ammonia levels, but this experiment incidentally worked well for studying DO.

Results and Discussion

My observations from the *N. maxima*, *N. albomarginata*, and *N. ampullaria* in the growth chamber provide some insight into the possibility that dissolved oxygen in pitchers is influenced by plant physiology, which is seen primarily in age-dependent differences in DO levels (Fig. 1). Pitcher age/condition has a significant effect on the DO of the experimentally added ddH_2O, specifically, in reference to mature pitchers, newly opened pitchers tend to have lower DO (correlation estimate =

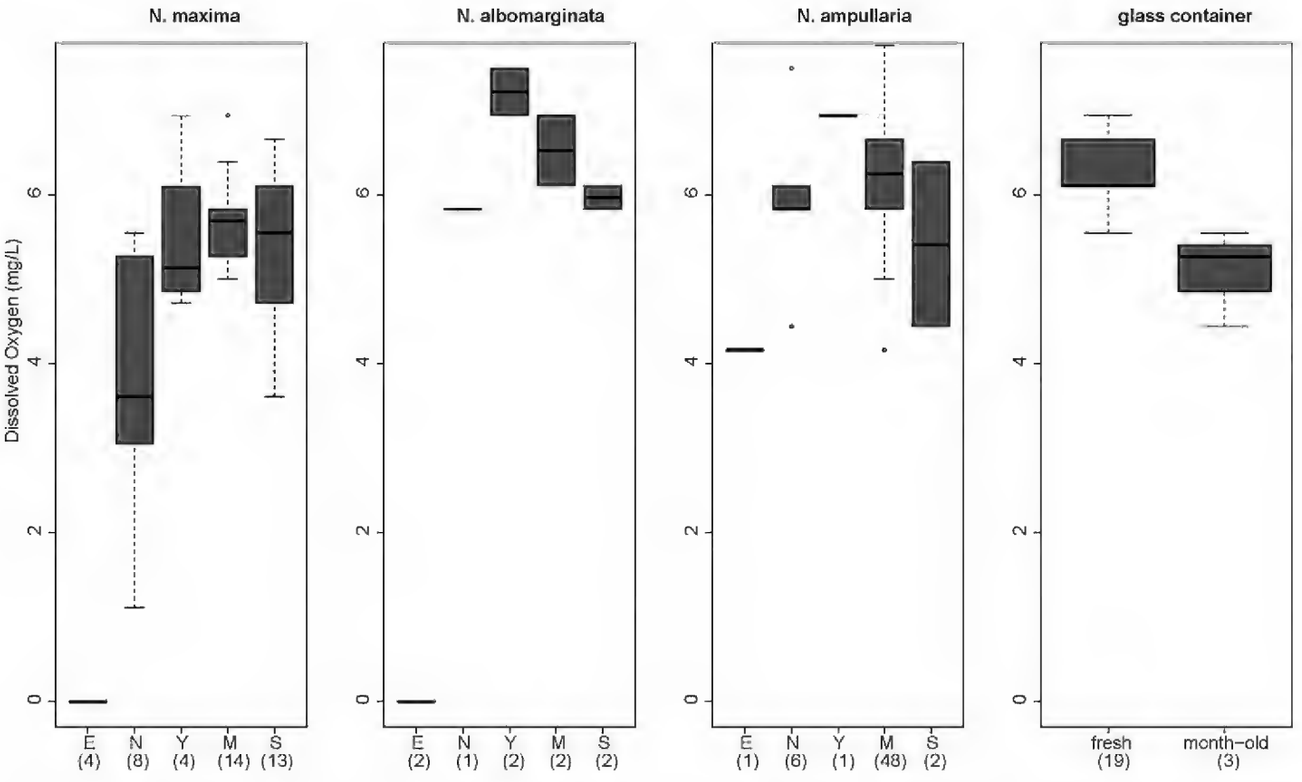

Figure 1: Results of 2013 growth chamber study, dissolved oxygen levels for the three *Nepenthes* species are broken down by pitcher age/condition, where E = endogenously-produced fluid in newly-opened (1-2 days post-opening) pitchers, N = "newly-opened" (<1 week post-opening) pitchers, Y = "young" (~2 weeks post-opening), M = "mature" (>2 weeks post-opening) pitchers, and S = "senescent" (brown/dying/dead) pitchers. For glass containers, "fresh" refers to ddH_2O DO measured less than one week after addition, and "month-old" refers to ddH_2O DO measured about one month after addition. Sample sizes for each pitcher condition or treatment is given underneath in parentheses.

-1.14, p = 0.0006), and likewise the endogenous fluid of newly opened pitchers has exceptionally low DO (correlation estimate = -5.41, p << 0.0001); senescent (browning/dead) pitchers have a slight, nonsignificant trend towards lower DO (correlation estimate = -0.53, p = 0.08), and young pitchers are not significantly different (correlation estimate = 0.20, p = 0.62). On the other hand, variation in DO levels cannot be explained by letting the water sit for different periods of time (p = 0.47 and 0.85 for week-long and month-long waiting period, respectively). The observations within these alternative waiting periods still vary according to the pitcher condition: for example, of the week-long waiting period samples, the DO of the 3 mature pitchers average 6.29 mg/L while DO of the 2 newly opened pitchers average 3.47 mg/L. Note that fully saturated water (i.e. water with 21% O_2) would hold an estimated 7.55 mg/L at 30°C or 8.26 mg/L at room temperature.

For glass containers, while not statistically significant (two sample t-test, t = 3.33, p = 0.06), month-old ddH_2O samples clearly reach lower DO levels than those taken from more freshly added ddH_2O examined no longer than a week after addition. The fresh ddH_2O in glass containers serves as a baseline for unmanipulated ddH_2O DO levels and the observations of month-old ddH_2O in glass shows that it takes at least a month for neutral processes (e.g. evaporation, microbial respiration) to drive down the DO in this context, and even then, it did not reach any lower than 4.44 mg/L. Thus, it is especially surprising that in less than 24 hours, ddH_2O added to certain pitchers can reach much lower levels than that (as low as 4.27 and 1.11 mg/L in senescent and new pitchers, respectively).

What I had expected prior to this study was that living pitchers would oxygenate their fluid and have higher DO than senescent pitchers, but what I found instead is that the youngest pitchers seem capable of rapidly deoxygenating their fluid, while older pitchers (whether healthy or senescent) stay within the normal DO levels seen in the glass controls during the short waiting period scheme. As pitchers in this experimental design were void of any insect inquilines and likely void of substantial microbial communities that could drive down DO with respiration, it is not possible to discern from this whether fluid oxygenation switches on in young/mature pitchers and then turns off in senescent ones—of note however, the sole month-old ddH_2O sample from a senescent pitcher reached the markedly low DO level of 3.61 mg/L while the month-old samples from healthy mature pitchers averaged 5.97 mg/L. While not conclusive due to small sample sizes, this is consistent with senescent pitchers acting more like inert containers and healthy pitchers actively maintaining higher DO levels over time. More conclusive here is the occurrence of active deoxygenation in newly opened pitchers. The pattern is best seen in *N. maxima*, which had the most even sampling, but the pattern of relatively lower DO in new pitchers can still be seen in the other two species (Fig. 1).

The most striking finding, alongside the hypoxic conditions in newly opened pitchers, is that the endogenous fluid within newly opened pitchers appears to be anoxic (0 mg/L) in all observations from *N. maxima* (4 samples) and *N. albomarginata* (2 samples). My one observation of endogenous fluid from a newly opened pitcher of *N. ampullaria* still followed the pattern of endogenous fluid having the relatively lowest DO within a species, but in this case, it was merely hypoxic at 4.16 mg/L.

Overall, DO did not vary significantly by species in this study (linear mixed model, p > 0.4 for each species). However, when comparing just the mature pitchers of *N. ampullaria* and *N. maxima* (no significant differences between either species and *N. albomarginata*, which has a very low sample size), *N. ampullaria* is found to have significantly higher mean DO here (t-test, t = 3.06, p = 0.005): 6.26 mg/L compared to *N. maxima*'s 5.69 mg/L. While I cannot firmly conclude from this that pitcher oxygenation is a trait that varies interspecifically across the genus, it could make sense for species that evolved specialized dietary strategies like *N. ampullaria* (Moran *et al.* 2003) to regulate their fluid properties in different ways. For instance, *N. ampullaria* is known to maintain milder pH levels compared to other species, which is believed to create a more permissive environ-

ment for the diverse community of insect inquilines that may help break down captured leaf litter (Moran *et al.* 2010). Similarly, maintaining oxygen-rich fluid could help sustain more inquilines. Perhaps the higher DO in the endogenous pitcher fluid of newly opened *N. ampullaria* compared to the anoxic fluids of the other two species indicates that *N. ampullaria* oxygenates more at all stages (as a caveat: it was more difficult to catch the exact moment of pitcher opening due to the uniquely narrow lid of this species, so that pitcher may have been open relatively longer before sampling than the other species).

Looking further into the potential of interspecific variation in pitcher oxygenation, I obtained data from 12 *Nepenthes* species and hybrids in the HortPark glasshouse in 2014: *N. chaniana* × *veitchii*, *N. clipeata* × *eymae*, *N. copelandii*, *N. densiflora*, *N. fusca*, *N. inermis* × *bongso*, *N. jamban*, *N. khasiana*, *N. muluensis* × *lowii*, *N. sanguinea*, *N. spectabilis* × *talangensis*, and *N. tentaculata*—though sample sizes within each species were generally low (Fig. 2). I did not find significant differences in dissolved oxygen concentrations by species (Kruskal-Wallis chi-squared = 14.124, p = 0.23), but there was notable variation across all pitchers, ranging from ~5% to ~30% oxygen (where atmospheric oxygen in the greenhouse was 21%).

I noticed a possible trend of upper pitchers having smaller DO values than lower pitchers (Fig. 3). Most species did not have multiple pitcher morphs available, and in most cases, there either was not a significant difference or enough replication to be meaningful. However, I obtained several

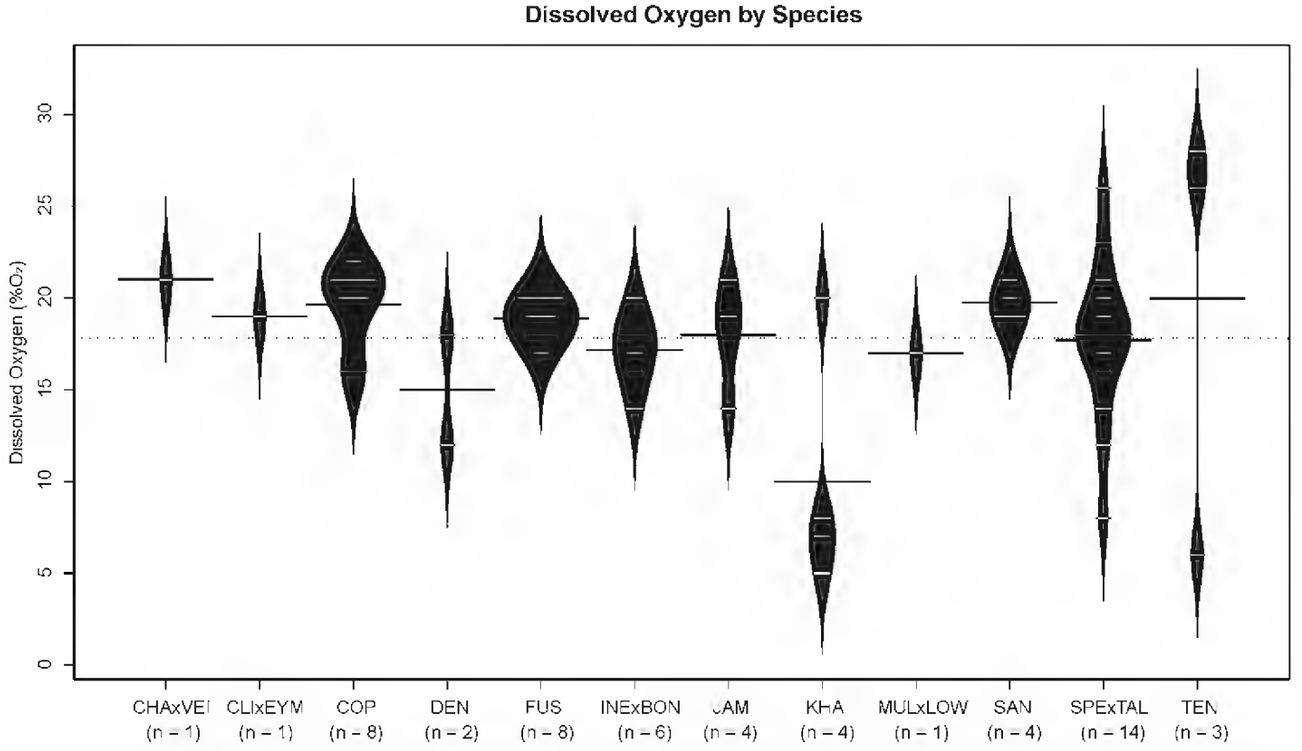

Figure 2: Beanplot showing results of oxygen measurements in 12 *Nepenthes* species and hybrids in the HortPark glasshouse. CHAxVEI = *N. chaniana* × *veitchii*, CLIxEYM = *N. clipeata* × *eymae*, COP = *N. copelandii*, DEN = *N. densiflora*, FUS = *N. fusca*, INExBON = *N. inermis* × *bongso*, JAM = *N. jamban*, KHA = *N. khasiana*, MUL×LOW = *N. muluensis* × *lowii*, SAN = *N. sanguinea*, SPExTAL= *N. spectabilis* × *talangensis*, TEN = *N. tentaculata*. Please note that names are based on 2014 taxonomic classifications (e.g. *N. fusca* is likely now *N. dactylifera*). Sample sizes for each species given below in parentheses. In the beanplot, thin white lines represent individual samples (length proportional to number of samples at a given DO) and thick black bar represents mean DO for that species. Dotted line indicates overall mean.

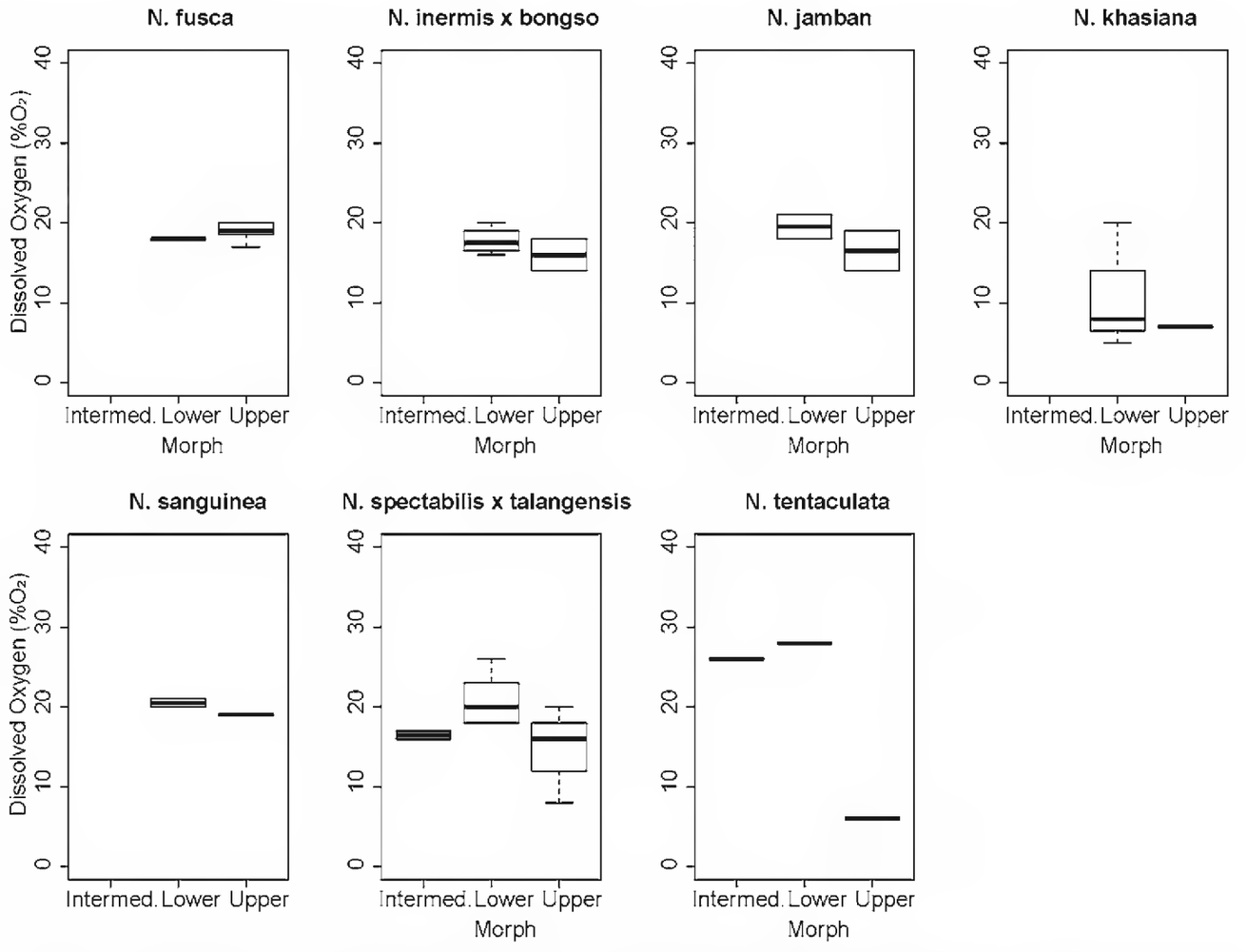

Figure 3: Boxplots of data from the 2014 HortPark glasshouse study, broken down by pitcher morph (upper, lower, or intermediate) for applicable species/hybrids.

datapoints for multiple *N. spectabilis* × *talangensis* plants containing upper, lower, and intermediate pitcher morphs, and the difference in means between upper and lower pitchers was significant in this case (t-test, t = -2.58, p = 0.03). While I only had one sample of each morph from *N. tentaculata,* the same trend can be found in that species as well (Fig. 3)—in both cases, lower pitchers have greater DO levels than upper pitchers, and the intermediate morphs notably fall somewhere in between. Note that most of the points that fall below 15% in Figure 2 are from upper pitchers (except one from *N. densiflora* and two from *N. khasiana*). Upper pitchers are necessarily younger than lower pitchers on the same plant, so I believe this trend may again indicate that more newly opened pitchers decrease their fluid DO.

Measuring DO in fluid from unopened pitchers of wild *N. gracilis* provided further support for the idea that younger pitchers normally have decreased DO levels. All five fluid samples were fairly hypoxic: 2.88 mg/L, 4.33 mg/L, 4.33 mg/L, 3.11 mg/L, and 3.77 mg/L, for a mean of 3.68 mg/L. This unopened *N. gracilis* fluid was not anoxic like I had previously observed in newly-opened *N. maxima* and *N. albomarginata* in the growth chamber, but still comparably hypoxic to the newly-opened *N. ampullaria*. Perhaps *Nepenthes* pitcher fluid in unopened/newly-opened pitchers is generally hypoxic, but different species vary in their minimum levels.

A possible mechanism that can explain how pitchers in their earliest stages of development deoxygenate their fluid is due to new pitchers releasing large amounts of gaseous carbon dioxide (Baby *et al*. 2017), this would flush oxygen out of the fluid; this process may cease as the pitchers mature, possibly giving way to increased input of oxygen from photosynthesis.

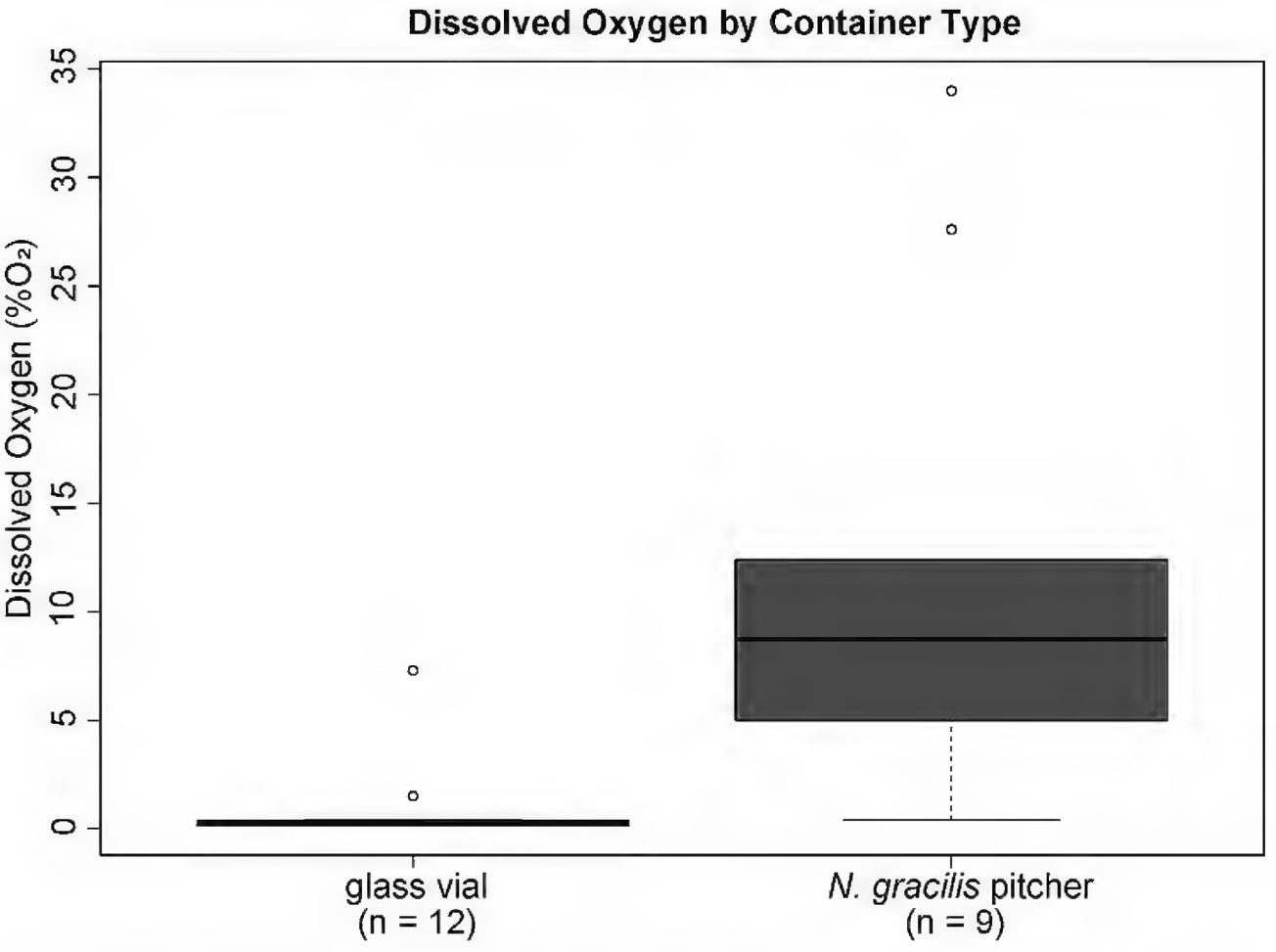

Figure 4: Results of the 2016 Raffles Institute greenhouse experiment, dissolved oxygen levels of pitcher fluid in glass vials and pitchers 18 hours after adding mealworm segment and insect inquiline treatments.

My most direct evidence of active oxygenation in healthy mature pitchers comes from the 2016 greenhouse experiment, where I had natural pitcher fluids with prey and inquilines (Fig. 4). I found significantly higher DO levels in pitchers than in glass vials (Kruskal-Wallis chi-squared = 12.16, p = 0.0005) showing both how quickly inquiline respiration can lead to severely hypoxic pitcher fluid in physiologically inactive containers (final O_2 levels falling mostly between 0.11% and 0.42%, where atmospheric oxygen in the greenhouse was 22.8%), and suggesting that the plants keep fluid oxygenated with photosynthesis that outpaces inquiline respiration. There were no significant differences in DO levels between the different insect inquiline treatments (Kruskal-Wallis test, $p > 0.05$), suggesting that the bulk of the oxygen consumption that occurred was due more to microbial respiration rather than insect respiration (though evaporation may also have played some role in oxygen depletion).

The near-anoxic conditions in the glass vials were sufficient to lead to death of the larvae, so pitcher oxygenation likely has fitness consequences for inquilines in the wild, allowing larvae to occupy fluids with substantial microbial populations that would be otherwise uninhabitable if not for oxygenation by the host plant. On the other hand, while hypoxic conditions in pitchers prior to opening may not be of consequence to inquilines when entry is impossible anyway, the persistent removal of oxygen that continues during the first few days after opening would be consequential to pitcher inhabitants. Perhaps these hypoxic conditions might benefit the plant by discouraging insect colonization too early on. Larval inquilines can act either as mutualists or parasites (Scharmann *et al.* 2013; Leong *et al.* 2018, 2019); perhaps larvae can be more beneficial when pitchers are mature

and full of prey, but when the pitcher is still new with limited prey, a growing larva could more easily steal more nutrients than it releases.

Conclusions

Nepenthes appear to be capable of actively oxygenating the fluid within their pitchers, analogous to what was already known for *Sarracenia*. Unexpectedly, I also found that unopened pitchers and pitchers in the earliest stages post-opening may actively decrease their DO levels (reaching total anoxia, at least in *N. maxima* and *N. albomarginata*). Oxygen regulation possibly varies by species, but the difference between pitchers of different ages seems more pronounced than interspecific differences. Understanding how fluid properties like DO are regulated by the plants has implications for understanding how the plant interacts with its symbionts (Adlassnig *et al*. 2011; Bittleston 2018; Gaume *et al*. 2019; Gilbert *et al*. 2020). Interspecific differences in DO regulation could very well contribute to the ability of pitchers to act as filters to shape what insects and microbes live within them.

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First observations of UV-induced fluorescence in *Heliamphora* (Sarraceniaceae) and other tepui flora

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Keywords: fluorescence, *Heliamphora*, morphology, phytochemistry, pitcher infauna, prey attraction, tepuis, visual ecology.

Abstract: Seven species of the carnivorous plant genus *Heliamphora* were studied in the wild across four tepuis of the Venezuelan Guyana. All were found to exhibit UV-induced blue fluorescence in their young and developing pitchers, the fluorescence being largely confined to the downward-pointing trichomes of the pitcher interior, with a small contribution from the nectaries. Subsequent work on cultivated plants confirmed the universality of this trait across all known members of the genus. Fluorescence microscopy localized the blue emissions to the surface of the trichomes and unequivocally showed that it represents true fluorescence. The phenomenon was found to be highly transient, generally being seen only in recently opened pitchers. Whether it has a biological function or is an incidental property remains to be determined. Possible roles in the attraction of prey and pitcher inquilines are discussed.

Introduction

Fluorescence, a form of photoluminescence, involves the absorption of electromagnetic radiation at shorter wavelengths and almost immediate emission at longer wavelengths. Once the source of excitatory radiation is extinguished, so too is the fluorescent emission, on a nanosecond timescale. In this it differs from phosphorescence, where the emitted radiation persists much longer (milliseconds to hours) and which has a different underlying mechanism.

Fluorescence in plants has long been the subject of scientific inquiry and the best-known example is undoubtedly that of chlorophyll *a*, which emits in the red to far-red, though blue-green plant fluorescence is also common. No studies on fluorescence in *Heliamphora* have previously been published, but a 2013 study by Kurup *et al*. claimed to show that three other carnivorous plant genera—*Dionaea*, *Nepenthes*, and the closely related *Sarracenia*—employ UV-induced blue fluorescence as a visual lure to attract prey. The results were widely reported, but concerns were soon raised about the study's methodology and conclusions. Clearly, more work is needed to elucidate the basis and functional importance (if any) of this phenomenon.

Methods

Field studies were carried out on seven species and one non-autonymic variety of *Heliamphora* across the summit plateaus of four tepuis: *H. chimantensis* on Apacará-tepui; *H. huberi*, *H. pulchella*, and *H. uncinata* on Amurí-tepui; *H. minor* var. *minor* and *H. minor* var. *pilosa* on Auyán-tepui; and *H. purpurascens* and *H. sarracenioides* on Ptari-tepui. Additionally, *Catopsis berteroniana* was imaged on the lower slopes of Auyán-tepui, and *Xyris* sp. and an undetermined Eriocaulaceae were photographed on the summit plateau of Ptari-tepui. Some species could only be studied in daylight

owing to their inaccessibility and therefore had to be artificially shaded prior to being photographed. A high-power UV hand torch with an emission peak of 365 nm was used in all cases.

All remaining species of *Heliamphora* that could not be studied in the wild were observed as cultivated specimens in the author's live collection. To confirm fluorescence, plants were viewed under the same UV torch as before.

Small pieces of tissue were prepared from a freshly opened *Heliamphora pulchella* pitcher from the author's collection. The resulting slides were viewed with a fluorescence microscope, being imaged under bright-field illumination as well as four different fluorescence filter cubes, with excitatory wavelengths ranging from UV to yellow.

Results

Field observations confirmed the presence of UV-induced blue fluorescence in seven species and one non-autonymic variety of *Heliamphora* (Figs. 1–3). Observations on cultivated plants of all remaining *Heliamphora* species showed that some level of blue fluorescence is exhibited by all members of the genus, though it is highly variable in its intensity, localization, and persistence (Figs. 4–5).

Under fluorescence microscopy, the retentive hairs were the only sampled parts of the trapping surface to show significant blue fluorescence under UV, with the surrounding epidermal tissue emitting no perceptible fluorescence (Fig. 6). This situation was largely reversed when the excitatory light was changed to blue and the emissions filtered to green, with the epidermal tissue showing strong green fluorescence in contrast to the weakly visible trichomes. Similarly, no trichome fluorescence was observed at the longer excitatory wavelengths. These microscopy studies unequivocally showed that the blue emissions represent true UV-induced fluorescence and not merely reflected blue light.

Wild *Heliamphora sarracenioides* pitchers were found to fluoresce internally despite lacking retentive hairs (Fig. 3). Subsequent observations revealed that *Heliamphora* pitcher nectaries also give off blue fluorescence, as does the nectar itself (Fig. 5).

Developing and freshly opened pitchers were found to be the most intensely blue-fluorescent due to subsequent quenching of trichome fluorescence. This quenching appeared to progress

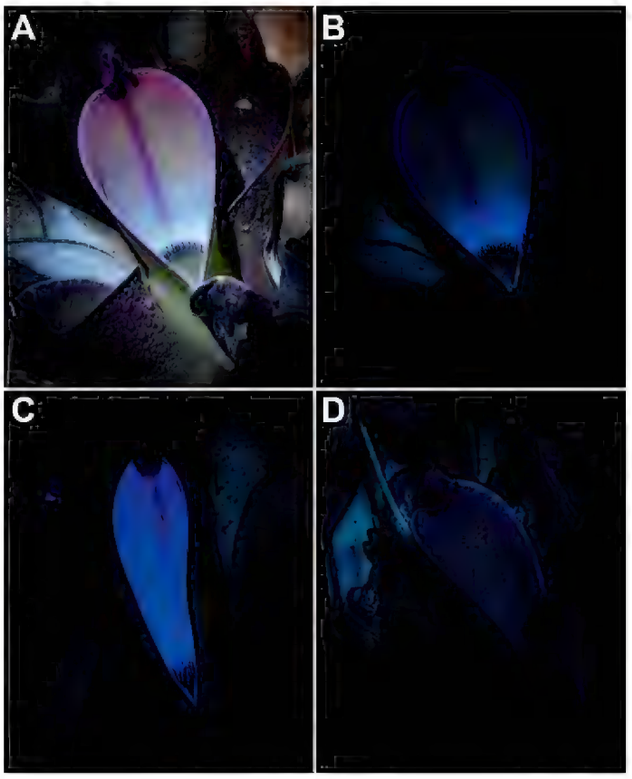

Figure 1: *Heliamphora chimantensis* on Apacará-tepui: (A–B) a freshly opened pitcher under white and UV illumination; here the majority of the inner pitcher surface lacks conspicuous blue fluorescence, the trichomes being confined to the area just above the waterline and to a narrow band lining the pitcher rim; (C) a pitcher in the process of opening; here the entire inner surface is lined with hairs and shows uniformly strong blue fluorescence; (D) an older pitcher from the same patch, showing no obvious UV-induced fluorescence (the pitcher is illuminated only by the small amount of visible light emitted by the UV torch, which necessitated a longer exposure).

Figure 2: *Heliamphora uncinata* at its type locality on Amurí-tepui. Strong blue fluorescence is apparent in the freshly opened pitcher; note that the older adjacent pitcher exhibited no perceptible UV-induced fluorescence whatsoever.

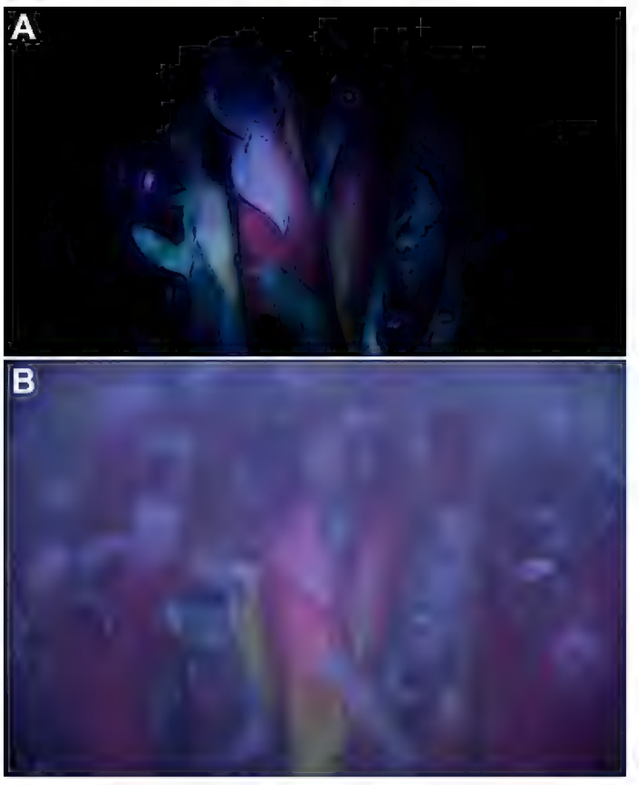

Figure 3: A freshly opened *Heliamphora sarracenioides* pitcher on the summit plateau of Ptari-tepui, (A) showing modest UV-induced fluorescence throughout the hairless interior surface (photo taken at 5:26 am local time). (B) The same clump photographed 14 minutes later (5:40 am local time). At this point, ambient light is already beginning to overwhelm the fluorescent signal (at least as perceived by human eyes).

very rapidly in most species, with the fluorescent signal rendered clearly diminished to non-existent within likely no more than a few weeks of pitcher opening. Of the species observed in the wild, this progression was most clearly seen in *Heliamphora chimantensis*, owing to its vigorous clumping habit. In pitchers of this species in the process of opening, the entire interior fluoresces brightly (Fig. 1C). Fully opened but still very young pitchers also fluoresce, but this is mostly confined to the ring of long hairs just above the fluid level (Fig. 1B). Fully pigmented adult pitchers (otherwise apparently completely functional) generally lack discernible fluorescence under 365 nm (Fig. 1D). Consequently, only a small fraction of functional pitchers fluoresce at any given time on any given plant (generally up to one pitcher per growth point and, in large clumps, as few as one per several dozen pitchers, as was observed in wild *H. chimantensis*). Fluorescence in *H. sarracenioides* was also found to be restricted to freshly opened pitchers, despite this species lacking retentive hairs (Fig. 3).

Preliminary observations revealed UV-induced blue fluorescence in a range of other tepui plants, including the carnivorous bromeliad *Catopsis berteroniana*, an undetermined Eriocaulaceae, and a species of *Xyris*. By chance, a single scorpion was found in association with pitchers of *Heliamphora purpurascens* on Ptari-tepui. It is likely to be the first scorpion ever recorded from the summit plateau of Ptari-tepui and probably represents a previously undocumented species. Scorpions are

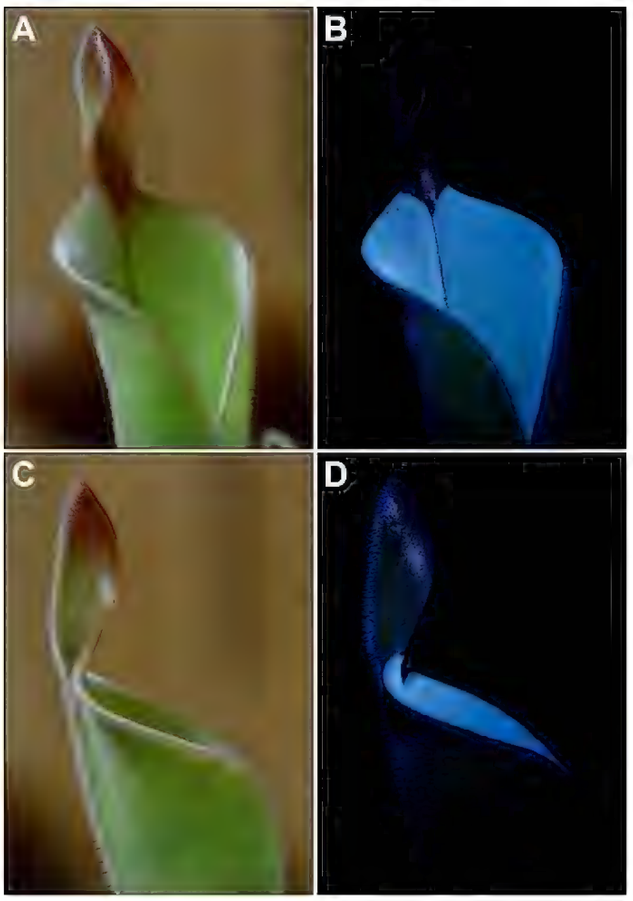

Figure 4: *Heliamphora parva* under white light and under UV in the dark. Note the modest blue fluorescence from the hairs of the exterior pitcher midrib (D).

not uncommon on tepui summits and, owing to their brilliant blue fluorescence, are among the animals most likely to be encountered during night-time fluorescence studies.

Discussion

Retentive hair fluorescence in *Heliamphora*: a biosignal?

The brilliant blue fluorescence of the retentive hairs is instantly captivating. Since retentive hairs are the primary structures involved in prey trapping, the question naturally arises: might they also play a role in prey attraction?

To be involved in biosignalling, the wavelengths of fluoresced light must lie within the sensitivity range of the putative target species. Most insects are trichromats, having visual sensitivity maxima in the UV, blue, and green wavebands. However, when it comes to ants, which make up the bulk of prey caught by *Heliamphora* in the wild, UV–green dichromacy appears to be the norm, with some limited evidence for UV–blue–green trichromacy. This would argue against a role in prey attraction, at least of ants, though in any case ants would seem an unlikely biosignalling target given their terrestrial nature

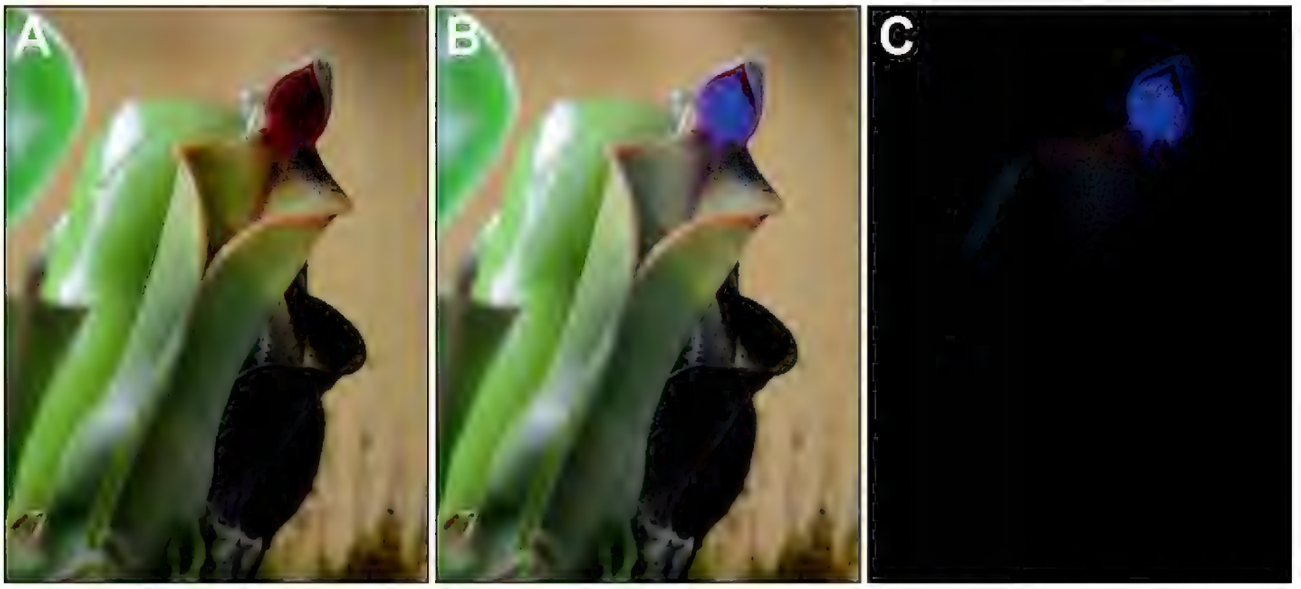

Figure 5: Cultivated plant of *Heliamphora nutans* from Yuruaní-tepui. This old pitcher lacked trichome fluorescence but showed strong nectar-derived fluorescence. The photos were taken under white light (A), a combination of white and UV light (B), and UV light alone (C).

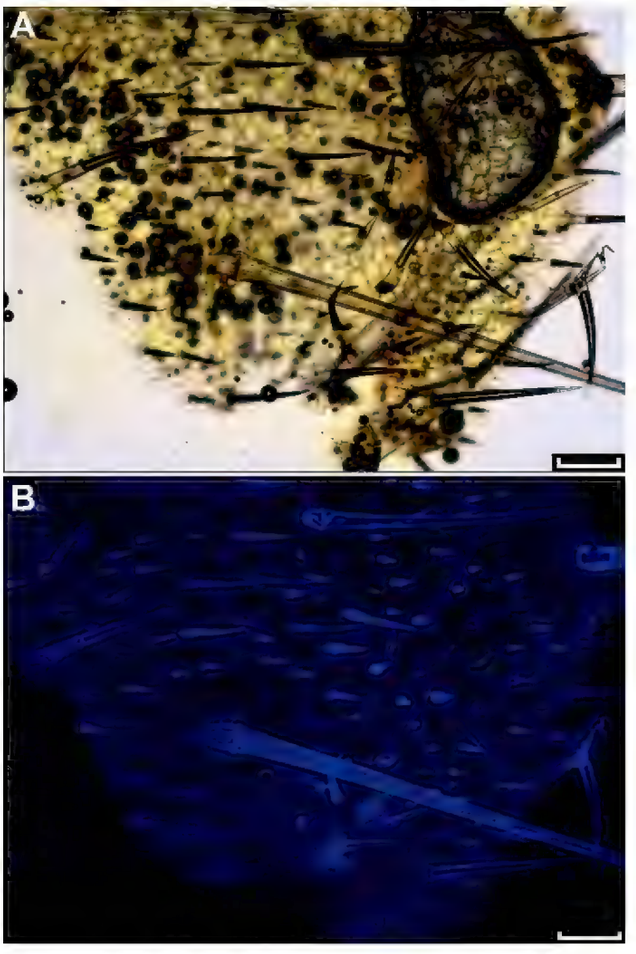

Figure 6: Thin slice of the interior surface of a young *Heliamphora pulchella* pitcher. At least two discrete size classes of trichomes are readily discernible. (A) As viewed under bright-field microscopy. (B) The same piece of tissue viewed under fluorescence microscopy with a DAPI filter cube (specimen excited by UV light and emitted light filtered to blue). It is clear that the trichomes are the only structures exhibiting significant blue fluorescence under this UV excitation range. Scale bars = 250 µm. (Image adjusted for the print article. See online article for original.)

and primary reliance on other sensory modalities. Further casting doubt on this idea is the brief temporal window of fluorescent activity, particularly when compared to the functional lifespan of an individual pitcher (many months to several years). On the other hand, assuming the ants can see the fluoresced wavelengths, early attraction might be sufficient, with subsequent capture facilitated by pheromone-based foraging trails. If the plant–ant interaction is a simple predator–prey relationship, attraction to blue fluorescence should not be selected for (unless a form of aggressive mimicry is involved), but if at the level of the ant colony it represents a mutually beneficial interaction then this would be expected.

Another possible function of retentive hair fluorescence might be early recruitment of pitcher inquilines. *Heliamphora* are known to commonly host mosquito (*Wyeomyia* spp.) and midge larvae, all of which are apparently obligate pitcher inhabitants. These likely benefit the plant by making nutrients from captured prey more readily available as part of a mutualistic relationship. One can see how it might be advantageous for ovipositing insects to be able to identify newly opened pitchers to ensure that their offspring (a) complete the aquatic stage of their life cycle before conditions deteriorate due to pitcher senescence and (b) are able to exploit the higher input of prey at the beginning of a pitcher's functional life. Likewise, the plant would presumably stand to benefit from having larval hatching coincide with the onset of prey acquisition. Indeed, it has been shown that mosquito (but not midge) oviposition overwhelmingly takes place in the very youngest *Heliamphora* leaves, even prior to the commencement of prey capture. A similar pattern has been consistently observed in the North American *Sarracenia purpurea*, which also hosts a *Wyeomyia* species in its pitchers, though in *S. purpurea* the inquiline mosquitoes are apparently attracted by chemical cues. Interestingly, color appears to be a factor in the selection of ovipositional sites by at least some bromeliad-breeding *Wyemoyia*, and multiple studies have demonstrated the same for other mosquitoes, including specific attraction to blue wavelengths.

Fluorescent biosignalling: a caveat

Caution should be exercised whenever attempting to assign ecological importance to fluorescent phenomena, since it is tempting to view them solely through the prism of human visual perception,

which often differs markedly from that of the putative target species. This is especially true when viewing UV-induced visible fluorescence at night under a high-power UV source, rather than in a biologically relevant context. The fluorescent 'glow' may appear impressive, but that is because the powerful excitatory (UV) light is invisible to us and so the comparatively weak fluoresced light is sensitizing eyes accommodated to darkness; when viewed under natural light the fluorescence is likely to become imperceptible (again, to us!).

The biological 'impracticality' of UV-induced visible fluorescence is down to both the inherent inefficiency of the fluorescence conversion process and to the low intensity of UV radiation reaching the Earth's surface as compared to visible light (the photon flux density of the former being around 5% of the latter). It is also important to remember that since UV radiation is visible to most insects, it can be utilized for biosignalling not only through fluorescence but also (much more efficiently) through reflectance. Similarly, a biosignal in the visible spectrum could be created by simply reflecting visible light. Of course, reflection and fluorescent signals need not be mutually exclusive, and it is possible that they act in concert to enhance or broaden the range of emerging (reflected plus fluoresced) light that corresponds to the visual sensitivity maxima of the intended recipients.

Other possible explanations

Fluorescence need not be ecologically relevant to have adaptive value. One possibility is that it is photoprotective, converting damaging UV-A radiation into less energetic blue wavelengths. Alternatively, blue fluorescence might enhance photosynthesis by 'creating' photosynthetically active radiation from otherwise unproductive UV light. There is evidence for both of these processes in corals and it is quite possible that they work in tandem in various green plants and lichens. In *Heliamphora*, however, neither role seems likely given the highly transient nature of the blue fluorescence and the small fraction of the total pitcher surface that fluoresces.

Finally, it is important to remember that many natural compounds and materials autofluoresce as a by-product of their chemical makeup. It is entirely possible that the observed fluorescence in *Heliamphora* is merely an epiphenomenon: an incidental, non-adaptive property of phytochemicals that evolved to serve some unrelated function.

Avenues for future research

To the author's knowledge, this paper constitutes the first published demonstration of fluorescence in *Heliamphora* or indeed any component of the specialized tepui flora. Further studies should be undertaken to confirm the chemical source of the blue fluorescence, characterize the timing and mechanism by which it is quenched, determine its excitation and emission spectra, and quantify the contribution of fluoresced light to total emerging blue light under various irradiance scenarios. The latter could then be related to known or inferred spectral sensitivities of ecologically relevant species (viz. prey and inquilines) to establish whether a biosignalling role is plausible. Ultimately, behavioural studies involving the putative target species would be needed to confirm fluorescent biosignalling. Potential non-ecological functionality, such as in photoprotection or photosynthesis enhancement, should also be investigated.

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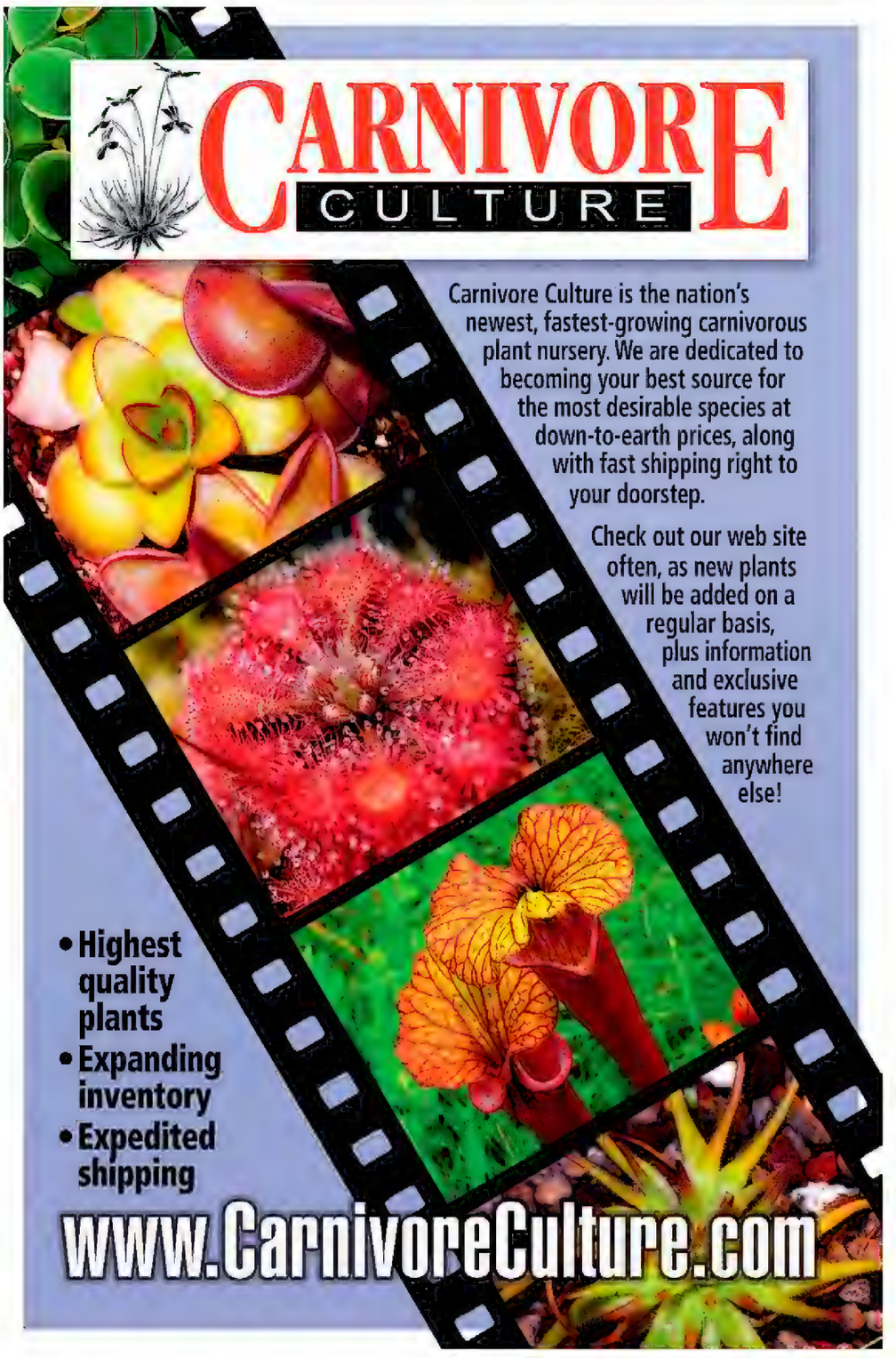
Golos, Michal R. 2020. First observations of UV-induced fluorescence in *Heliamphora* (Sarraceniaceae) and other tepui flora. Carniv. Pl. Newslett. 49(4): e1-31.

https://cpn.carnivorousplants.org/articles/CPNv49n4pe1_31.pdf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Drosera capensis: some variation in cultivation and in the wild

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Introduction

The Cape Sundew (*Drosera capensis* L) is one of best known and most widely grown of all the sundews. It's large size, mobile leaves that fold over prey, and ease of cultivation have made it a popular carnivorous plant to grow and study. Yet it remains poorly known in the wild. To help remedy this, I present a summary of my observations of *Drosera capensis* in nature, from the study of herbarium specimens and the literature, and cultivated plants to present a current picture of its variation in cultivation and in the wild.

Figure 1: Plant of *Drosera capensis* at Silvermine Nature Reserve.

Drosera capensis is a robust perennial sundew that is native to South Africa, and which has been described in detail in recent literature (e.g. Robinson *et al*. 2017). Plants generally form a semi-erect rosette to about 25 cm diameter of narrowly rectangular leaves to about 16 cm long, that often sit aside a short stem (Fig. 1). Flowers are produced on a scorpioid cyme that has spreading colorless hairs on its peduncle. Each bloom is about 2 cm across, and usually has pale purple petals. The ovary is surmounted by three sub-horizontal styles that are bifurcated from the base and expand into a terete to an irregularly obovate stigma. Flowers are self-fertile, and autogamous and usually set an abundance of highly viable dark brown seeds that are cylindrical in shape and around 0.6-0.8 mm long by 0.1-0.15 mm maximum diameter. Seed ripens 4 to 5 weeks after pollination.

Distribution and Ecology

Despite its strong association with the Western Cape, the Cape Sundew is a widespread species that grows along the entire south coast and adjacent sandstone ranges of South Africa; between Port Elizabeth and Cape Town. It also extends to about 230 km north of Cape Town along sandstone ranges to Gifberg (Obermeyer 1970) (Fig. 2). This is a species of permanently wet habitats where it is commonly found in permanent seepage zones; in thin moss-covered rock or pockets of alluvium on stream banks or the sides of farm dams; and in peaty soil on the edge of coastal wetlands. It grows from sea-level to about 1800 meters altitude. Plants in the higher elevation sites experience frosty winters and so often have a period of winter-dormancy where they die back to a dormant growing point.

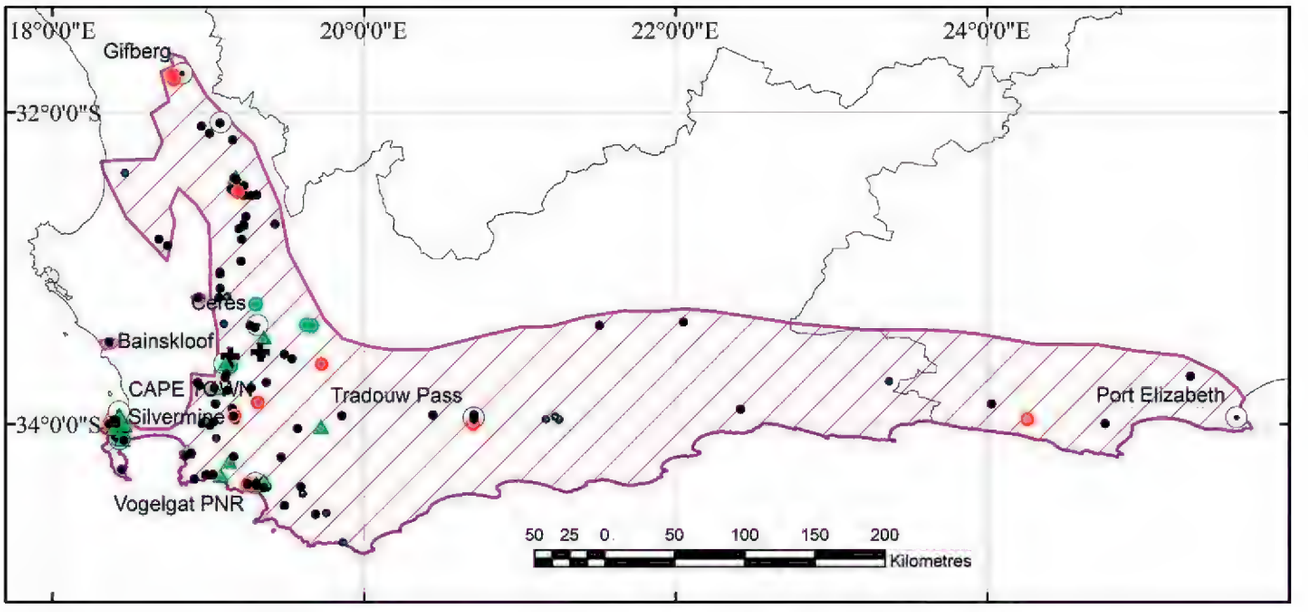

Figure 2: Distribution map of *Drosera capensis* records. Symbols used wide-leaved form (green triangle), red-leaved plants (red circle), mini-plants (pale blue circle), narrow-leaved form (black dots), and Bainskloof form (black cross). Records from the Compton Herbarium, iNaturalist, Obermeyer (1970), and my own observations.

Despite its legendary fecundity, the Cape Sundew is often uncommon and localized in the wild. In September 2017, I saw an exception to this, where *D. capensis* was the dominant herb over at least a hectare of shrubland in a seep in the Tradouw Pass, about 200 km east of Cape Town (Fig. 3). Sundews grew in abundance after a recent fire had reduced the canopy of the shrubland to an array of slowly-resprouting bare trunks. *Drosera capensis* was absent from nearby seepages, most of which had also burnt, even though *D. aliciae* grew in all local wetlands. It is not clear what keeps

Figure 3: *Drosera capensis* in the Tradouw Pass.

D. capensis in check in the wild; its widespread distribution suggests that this species needs more than wind or moving water to spread its seeds over hostile territory. It is curious that this sundew did not spread north of Port Elizabeth, as *D. natalensis* has done.

The Current Classification

Adrian Slack (1986: p. 44) described two distinct forms of *D. capensis*: the 'narrow-leaved' form and the 'typical' form which here will be referred to as the 'wide-leaved' form. These forms differed in relation to the following characters: leaf width; relative widths of the lamina to the petiole; relative lengths of the lamina to the petiole; degree of stem formation; and petal color. To this two-fold informal classification, D'Amato (1998: p. 127-129) added three additional forms, based on plant color and stature: the 'alba', 'red', and 'narrow' forms. It is possible that D'Amato's 'narrow' form may be equivalent to Slack's 'narrow-leaved' form. Further variants have been suggested since then, based primarily on putative location of origin. However, with few exceptions, it is challenging to assign an unlabelled plant to the available informal names due to the short descriptions of each form, and the phenotypic plasticity exhibited by this species (Wang *et al.* 2015). For this article, leaf dimensions cited are from the longest leaves, produced in early summer. Floral details are required for identification.

'Wide-leaved' form

The 'wide-leaved' form is the robust version of the species in which the lamina and petiole are both are more than 3 mm wide and in the petiole is about 60% the width of the lamina (Fig. 4). The lamina is defined by the presence of insect-trapping hairs, is about the same length as the petiole, and is up to 8 mm wide. The underside of the leaves has a sparse cover of colorless eglandular hairs. Flowers are large, often around 3 cm diameter with broadly ovate overlapping petals that are usually dark purple in color. The stigmas are irregularly obovate to elliptic and widen conspicuously from the terete style segments. These plants slowly develop conspicuous stems to 15 cm tall. This form is also known as the 'broad-leaf' form (GrowSundews.com 2020). Also, many of the 'giant' plants in cultivation are of this form.

Figure 4: 'Wide-leaved' form of *Drosera capensis*, with the lamina almost twice as wide as the petiole, and both more than 3 mm wide.

This form is restricted to the south western part of the Western Cape where is has been recorded at the Silvermine Nature Reserve, Vogelgat Private Nature Reserve, and the former Bergvliet Farm (now part of urban Cape Town). Plants from Vogelgat in cultivation often have pale purple flowers.

'Narrow-leaved' form

The 'narrow-leaved' form Slack (1986) describes plants with leaves to about 12 cm long that are of uniform width, or with the lamina up to twice the width of the petiole; and in all cases the leaf is

no more than about 3 mm wide. The lamina is about the same length as the petiole and is up to about 3 mm wide. Leaf eglandular hair cover is similar in density and location to the 'wide-leaved' form. Mature plants may have no obvious stem, but older plants can form stems to 5 cm long. The overall plant color is olive green, to reddish. The flowers are about 2 cm diameter and have pale purple petals and terete to narrowly ovate stigmas. This description matches the usual form of the species in the wild, and which has been in cultivation for decades.

Red-leaved plants

Since at least 1991, red-leaved plants of *D. capensis* have been available in cultivation (ICPS seedbank list, 25 April 1991). These plants are almost identical in size and morphology to the 'narrow-leaved' form but the plants turn vibrant red under bright illumination (D'Amato 1998). The leaves in plants cultivated here grow to about 10 cm long, divided almost equally between lamina and petiole, and with few eglandular hairs on the leaf under surface. Flowers are up to 2 cm across and have style segments that are dark purple in color and irregularly ovate stigmas.

Most red-leaved plants in cultivation are likely to have come from a roadside seepage site at Gifberg, at the northern end of the species range (Fig. 5). However, red-leaved plants are known from other locations, such as at Travellers Rest, the Koue Bokkeveld plateau, and on Table Mountain (iNaturalist 2020) (Fig. 2). Further study is recommended to see how many of these populations of red-leaved plants have a genetically fixed trait to express red pigmentation or are responding to a transitory stress, such as increased light levels or nutrients following fire.

Figure 5: Red-leaved plant at Gifberg.

This form of *D. capensis* was the first sundew to have it full genome determined and published (Butts *et al.* 2016). During September 2017, I was able to show the main authors of the paper the plants in the wild.

White-flowered plants

White-flowered plants of *D. capensis* appears to have emerged spontaneously in cultivation in Western Europe in the 1980s and spread rapidly from there (D'Amato 1998). It is sometimes called *D. capensis* 'Albino' (GrowSundews.com 2020). Leaf morphology fits with the 'narrow-leaved' form of the species. Its flowers are 10 to 14 mm diameter with white petals and moderately expanded stigmas (Fig. 6). The leaves are a golden green color. The insect trapping hairs have colorless stalks and green to pale red

Figure 6: Flower of the 'white petal' form also showing its typically dilated stigmas.

glands. Such plants have not been reported from the wild. However, I did see white-petalled plants in the Mendocino bog in northern California in August 2018 that may have been deliberately introduced, given the history of the site, rather than having arisen spontaneously from the naturalized population of 'narrow-leaved' form plants there.

Plants with additional insect-trapping hairs

The occasional plant may have additional insect-trapping hairs on one of two organs: the bracteoles and the petals. Occasionally some otherwise typical 'narrow-leaved' form plants develop enlarged bracteoles on the scape that have insect-trapping hairs (Fig. 7A). I have seen such plants in the wild in the Koue Bokkeveld plateau with Eric Green in 1998. This character occurs in some other species of *Drosera* too, where it may be widespread enough for such plants to be formally recognized, such as *D. rotundifolia* var. *bracteata* from Corsica (Baffnay *et al*. 1985).

The first flowers of a scape of some red-leaved plants develop a row of insect trapping hairs along the mid-vein of the petals (Fig. 7B). It is not known if such glandular hairs have the power of digestion.

Mini-plants

Plants no more than 10 cm diameter when mature have been in cultivation for at least 20 years. These plants produce small olive-green semi-erect rosettes to 10 cm across with a congested stem at most a few cm long. The petioles are 1.5 to 2 mm wide and the lamina are 3 to 4 mm wide. The scape is not proportionately reduced in size compared to the rest of the plants and so towers over the rosettes and has dark purple flowers to about 2 cm diameter.

Figure 7: (A) Scape of a plant with enlarged glandular-hairy bracts. (B) Some red-leaved plants produce flowers with a partial row of insect-trapping hairs along their mid-line.

This poorly known variant has been recorded from the highest peaks around Ceres and Bainskloof, such as Matroosberg, and the upper slopes of Baviaanskloof between about 1000 and 1800 m altitude respectively. Plants of typical form also occur in this region, and with overlapping altitudinal range, so it is not technically an 'alpine' form but it has many 'alpine' attributes, such as the ability to survive frosty winters with periodic snow falls by dying down to the growing point that is protected by persistent bracts and thermal insulation from the wet habitats in which it grows.

Eric Green had a fascinating tale of the adventure to Matroosberg where he found plants of this form – the likely source of many in cultivation. During this adventure, Eric recounted how each time he thought he was near the top, another slope to climb was revealed. He was with his young grandson who had not seen snow before, and so enjoyed playing in snowbanks; while Eric kept an eye out for chance of encounters with unfriendly wildlife.

Travellers' Rest plants

In September 2017, I observed very large plants of *D. capensis* on the banks of the Doring River at Travellers' Rest – east of Clanwilliam (Fig. 8). The plants formed rosettes to about 30 cm across. The petioles were about 2 mm wide, and the laminas were about 3 mm wide. The petioles were longer than the leaf blade. Some plants at the site were fully red in color. Many plants were in flower and had pale purple flowers about 1.5 cm across, with terete style segments.

A number of plants in cultivation share the trait of the plants at Travellers' Rest by producing leaves with a petiole longer than the leaf blade; up to twice the length. This is the other source of the 'giant' plants in cultivation. Such plants are like a long-leaved variant of the 'narrow-leaved' form.

Figure 8: Robust plants of *Drosera capensis* from Travellers' Rest form rosettes to 30 cm across.

Paddle-shape leaved plants

Plants with lamina to around 6 mm wide on petioles to 2 mm wide do not fit neatly in the informal two-fold classification. I saw such plants at the top of the Gydo Pass, near Ceres, in September 2017 where plants grew in a sphagnum slurry on the edge of a dam at about 1000 meters altitude. The site experiences frosty winters and the plants were coming out of dormancy. They formed sparse rosettes of semi-erect leaves that reminded me of *D. anglica* plants (Front Cover). Due to the sodden nature of the site, new plants were seen to spontaneously emerge from older leaves where they were submerged.

A form of paddle-shape leaved plant is known from Bainskloof Pass. These plants also have a distinct internode so that these plants quickly form a conspicuous stem (R. Maharajh, pers. comm., 2020) (Fig. 9). I have yet to see plants of this form. When I looked for such plants in 2017, I saw that *D. capensis* grows in seepages along about 20 km of the R301 road that goes through Bainskloof Pass. However, all of the plants I saw at the time were of the typical 'narrow-leaved' form, which suggests that the stem-forming plants are of limited distribution. Caulescent plants with paddle-shaped leaves have been found recently at Waaihoekskloof, near Ceres, about 20 km east of Bains-

Figure 9: Plants of the "Bainskloof form" of *Drosera capensis* showing the characteristic paddle-shaped leaves and distinct internodes. Plants grown and photographed by R. Maharajh.

kloof (iNaturalist 2020). Similar plants have also been reported from Montague Pass, about 400 km east of Cape Town.

I have grown another 'paddle-leaved' form of *D. capensis* for many years which until recently I had mistaken for the Bainskloof form. However, this form has congested internodes and so forms a stem only very slowly. The leaves are to 6 cm long, with a petiole to 1 mm wide and leaf blade to 3 mm wide, and they are noticeably spirally arranged on the stem. The underside of the leaves is covered with abundant eglandular hairs. The flowers are up to 1.6 cm across and have dark purple petals. The stigmas are dark purple and are irregularly obovate in shape. This form of the species came from Richard Sullivan, but it is not clear where it came from in the wild.

Summary and Conclusions

Drosera capensis is a well-known and widely studied species due to its large size, dramatically mobile leaves, and ease of cultivation. However, the link between cultivated plants and plants in the wild has been rarely described, so that it has not been made clear before that the 'typical' ('wide-leaved' form) plant in cultivation (sensu Slack 1986) is not the typical form of the plant in the wild.

I present a summary of some of the natural variation in the species and hope I have presented a framework to better understand this beautiful sundew; one that has many more secrets to reveal.

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Hypothesis of tumbleweed-like dispersal of *Drosera* seeds

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Erect-growing tuberous sundews of *Drosera* subgenus *Ergaleium* section *Ergaleium* produce seeds of diverse size and shape (Lowrie 2013). Seeds produced by such species as *D. andersoniana*, *D. macrantha*, and *D. pallida* are large and winged, and fit the classic model of those dispersed by the wind (Lowrie 2013: Vol. 2, p. 508), i.e. pterometeorochory. However, many species in this section produce small, round seeds (e.g. *D. gigantea*, *D. salina*, and *D. yilgarnensis*) that appears better suited to dispersal by gravity or water than by the wind. So how do you explain how these taxa spread across the landscape when some of their seed appear to be poor candidates for long-distance dispersal?

The situation is trickier when you consider that most tuberous *Drosera* are self-incompatible; that is, they need genetically compatible plants from different seeds to grow and flower in close proximity to enable cross-pollination. The long-distance dispersal of large, winged *Drosera* seed comes with low likelihood that seeds will land close enough together for any resulting plants to cross-pollinate. And yet, large and fecund populations of these sundews occur, often separated by hostile territory.

A characteristic feature of *Drosera* flowers is that the floral parts are retained after anthesis (Fleischmann *et al*. 2018). The petals wither and often cover the apex of the fruit. The sepals also enclose the fruit. This results in small gaps through which individual seeds may fall. However, seed is often retained in the dry fruit.

During fieldwork in south western Australia in October 2019, I made observations that revealed a way in which these sundews may disperse seed across the landscape, and to do so in a way that better guarantees resulting plants will form viable populations.

Conditions during recent fieldwork were warmer and drier than usual, and so many sites I visited had dried out and plants were dormant. The dead remains of tuberous *Drosera* dry black or dark brown and were readily visible amongst the other herbs. Over time they detach from the ground. However, the upper parts of many of the climbing species (such as *D. macrantha*) were still attached to surrounding vegetation. Importantly, many of the plants had seed in their fruit.

At Lake Hurlstone, near Hyden, most dead plants of *D. zigzagia* stood where they had grown. But many had been detached and had been blown into small piles against barriers (Fig. 1). This species has elongate seeds that is likely to be blown some distance on the wind. But it grows on the edge of salt lakes – an environment hostile to seeds that land there. The same applies to *D. salina*, from the same environment and region, but it has small round seeds that have very low chance of long-distance wind dispersal. Instead, I propose here, that long-distance dispersal of these species may also be facilitated by the transport of detached plant parts, with seed, by the wind – in a manner more akin to some grasses (such as *Panicum effusum*) that may be air-born for part of the journey than as a true tumbleweed (*Salsola* species: Chenopodiaceae), i.e. chamaechory. This has the added advantage of increasing the chance of groups of compatible plants getting established in close proximity. Given most plants would be closely-related, this would be a driver for potential speciation.

During fieldwork I also observed that even those sundews with seeds classically adapted for wind pollination often grew as isolated groups. This suggests that a proportion of these seed stays close to the parent plant. This offers the same advantage of a higher chance of seed set. It also suggests that long-distance wind-dispersal of plant parts with seeds may be a rarer event than for smaller taxa in exposed situations.

Figure 1: *Drosera* zigzagia near Hyden. Dead plants with seed have been detached, moved, and formed small piles against barriers, and appear to be an example of chamaechory.

This hypothesis is yet another way (Gibson 2015) that seeds of sundews may be spreading around the landscape. It suggests that the seeds of some taxa have multiple ways of traveling over a landscape, and to increase the chance of founding new populations.

Acknowledgement: I thank Allen Lowrie for discussions on the subject of *Drosera* seed dispersal that have kept me thinking about this interesting topic.

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Witanowski's discovery - and how its early misinterpretation and subsequent neglect continue to impede scientific progress and insight

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Keywords: *Drosera*, phytochemistry, naphthoquinones, chemotaxonomy.

Abstract: W.R. Witanowski isolated and characterized the naphthoquinone ramentaceone from *Drosera rotundifolia* in 1934 and named the compound droserone. This constitutes the first publication that described the correct detailed structure of the main naphthoquinone in a sundew species, the first publication that identified ramentaceone as a natural product, and the first publication to introduce the name droserone for this naphthoquinone. Nevertheless, none of these facts is reflected appropriately in the literature until now. This prompts a reappraisal.

Introduction and some general remarks

The history of science is popularly portrayed as a series of success: cognitive improvements linked to each other by logic, and experience (frequently mistaken for knowledge) is stated to be the basis for "educated guesses", the hypotheses that – in the case of natural sciences – need to be tested (ideally, confirmed) by (ideally, ingenious) experiments. A somewhat less positivistic view has science as the laborious process of correcting mistakes, the discovery and elimination of previous failures, some of which are surprisingly influential in hindsight. While either perspective has a certain justification, both underestimate the influence of the interested parties, humans with intentions, opinions, and bias.

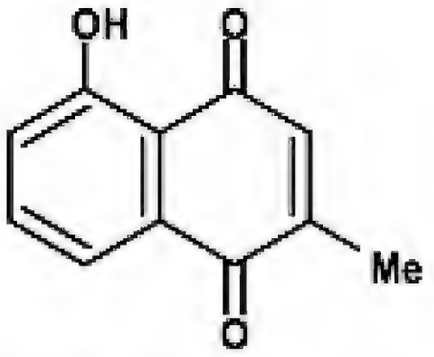
It is the aim of this note to correct a few mistakes that occurred early in the exploration of the chemical constituents of sundews, to rehabilitate an important researcher in this field and to explain how this all affects our current understanding of the matter.

Witold Rawita-Witanowski (1899-1945), biochemist, neurophysiologist, and pharmacologist, was the last Dean of the Faculty of Pharmacy at the University of Warsaw in the pre-war time (Witanowska & Wroczyński 2018), and his most important discovery in the context of carnivorous plants became a victim of its historical circumstances (in which German colleagues played an unfortunate role; being German, the present author hopes this text will help to set some of this injustice straight) just like the person became a victim of the murderous German regime after the Warsaw Uprising.

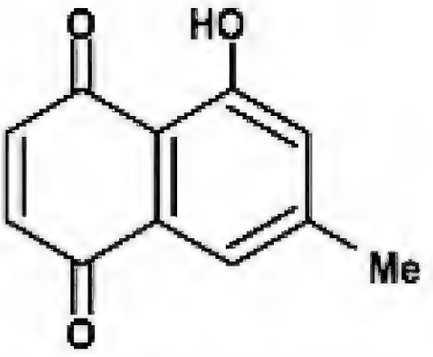
The (apparent) state of play until 2020

The acetogenic naphthoquinones, plumbagin (5-hydroxy-2-methyl-1,4-naphthoquinone, 2-methyljuglone, P in this paper, cf. scheme 1) and ramentaceone (5-hydroxy-7-methyl-1,4-naphthoquinone, 7-methyljuglone, M in this paper), are important chemotaxonomic markers in sundews (*Drosera* L., Culham & Gornall 1994, Schlauer *et al.* 2017, 2018) because most species contain only one (main) isomer or no naphthoquinone at all; both isomers together (at equal amounts) are almost exclusively found in hybrids between quinone-heterogenous species (Schlauer & Fleischmann 2016). The distribution of the isomers in the genus (Zenk *et al.* 1969) has demonstrated their chemotaxonomic significance.

Scheme 1:



Plumbagin (P)



Ramentaceone (M)

According to experts in the field (Thomson 1957), within Droseraceae P was first isolated from *Drosera rotundifolia* (Witanowski 1934, Dieterle 1935), *D. binata* (Dieterle 1935), *D. peltata* (Asano & Hase 1943), and *D. intermedia* (Denoël 1949).

M was apparently (Thomson 1971) discovered in sundews much later, after it was first identified and distinguished from P in *Diospyros* (Cooke *et al.* 1952), in *Drosera* "ramentacea" (Paris & Delaveau 1959; later identified as *D. madagascariensis*), *D. intermedia* (Bendz & Lindberg 1968), *D. aliciae* and *D. capensis* (Zenk *et al.* 1969). As evident from the annotation, already the early history was heavily compromised by wrong species identification, but as we shall see swiftly, also the chemical structures assigned to the isolated compounds were more guesswork guided by misleading expectations than evidence-based elucidation.

The true story or what went wrong, what is wrong and why

In his ground-breaking (but unfortunately, fundamentally and frequently misunderstood) work, Witanowski (1934) demonstrated by an unambiguous degradation reaction that the compound he isolated from (correctly identified) *D. rotundifolia* and that he called droserone was a naphthoquinone with a methyl group in the phenolic ring (*i.e.*, not in the quinoid ring!). In contrast, the isomer P has the methyl group in the quinoid ring.

In other words, Witanowski (1934) was the first to determine the correct constitution of M as a natural product, and the first trivial name of the compound was droserone. The fact that Dieterle (1935) attributed the (wrong) P structure to the quinone from the same species only a few months later was most probably caused by his simultaneous investigation of another species (*D. binata*, that really contains P) and the (wrong) assumption that one genus could only contain one characteristic quinone. For various reasons, Dieterle's (wrong) and not Witanowski's (correct) conclusion on the structure of the main naphthoquinone from *D. rotundifolia* prevailed and persisted. Also Witanowski's name droserone was (again, only a few months later!) used for a different compound, viz. 3-hydroxyplumbagin (3,5-dihydroxy-2-methyl-1,4-naphthoquinone, Macbeth *et al.* 1935, first detected in *D. whittakeri* by Rennie 1887), and this later homonym persists in the literature.

Only the entirely wrong interpretation and the subsequent neglect (essentially caused and initiated by Dieterle 1935) of Witanowski's (1934) results made later investigators think they (Cooke *et al.* 1952) had determined the structure of M for the first time or they (Paris & Delaveau 1959) had the obligation to give it a new trivial name, or even made them (Macbeth *et al.* 1935) use Witanowski's original name droserone for a different compound that is ironically again derived from the opposite isomer P. Witanowski was thus the researcher who in reality made the first discoveries for which not less than three different, subsequent publications claimed priority, all of which based essentially on the erroneous claims in a fourth subsequent publication!

Although it was indicated from the beginning (Bendz & Lindberg 1968) that M was only a trace constituent of *D. intermedia* (the main isomer in this species being P), some authors (Zenk *et al.* 1969) only mentioned the minor constituent, which resulted in considerable confusion in the subsequent literature (Egan & van der Kooy 2013).

The proposed and the actual structures and names with the respective references are summarized in the following table.

Source species	Reference	Name used for Quinone in Reference	Isomer actually found
Drosera rotundifolia	Witanowski 1934	Droserone	M
D. whittakeri	Macbeth *et al.* 1935	Droserone	3-Hydroxy-P
D. rotundifolia	Dieterle 1935	Plumbagin	M
D. binata	Dieterle 1935	Plumbagin	P
D. peltata	Asano & Hase 1943	Plumbagin	P
D. intermedia	Denoël 1949	Plumbagin	P
D. "ramentacea"; later identified as *D. madagascariensis*	Paris & Delaveau 1959	Ramentaceone	M
D. intermedia	Bendz & Lindberg 1968	7-Methyljuglone, Plumbagin	M (trace) + P (main)
D. aliciae, *D. capensis* and several other spp.	Zenk *et al.* 1969	7-Methyljuglone	M
D. binata, *D. whittakeri* and several other spp.	Zenk *et al.* 1969	Plumbagin	P

Even more recently, in a fairly successful attempt to revise the structure and biosynthetic origin of an indanone derivative of P from *Triphyophyllum peltatum* (Ishii *et al.* 2019), Witanowski was credited for having isolated the P derivative droserone (use of the name in the sense of Macbeth *et al.* 1935, not Witanowski 1934) from *D. rotundifolia*. As the (main) isomer found in *D. rotundifolia* is M and not P, this reference led the author of the present note to study the original source, which resulted in the discoveries outlined above.

Conclusions

The lesson to be learned from this story is simply what **should** be general practice in science, viz. to read, understand, and appreciate what colleagues (irrespective of the respective persons' social status or provenance) have achieved in one's field. This includes proper citation. As a practical consequence, we should recognize Witanowski (1934) as the first researcher who correctly identified a specific naphthoquinone (M) from a carnivorous plant (and thus, the first who isolated and identified M from a plant whatsoever). His designation "droserone" (for M) did unfortunately never gain general acceptance among chemists, and as it is now the "standard" trivial name for a different compound (Macbeth *et al.* 1935), its original meaning should rather not be restored because this would cause more confusion than clarity. Instead, the later (Paris & Delaveau 1959) proposed name "ramentaceone" (although it was originally derived from a confused source species) is sufficiently descriptive, widely used and unambiguous to replace Witanowski's "droserone".

Acknowledgements: When this note was written, the scientific community was severely affected (and not so much infected) by a coronavirus pandemic and particularly so by the administrative measures taken to prevent its further spread. This caused some hardship in obtaining essential literature, and for this reason I am particularly indebted to my colleagues who helped to gather what was required for this text. I would especially like to express my sincere gratitude to Jaromir Budzianowski, Poznań, Heiko Rischer, Helsinki, Lubomir Adamec, Třeboň, and Maciej Strzemski, Lublin.

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New cultivars

Keywords: cultivar, *Dionaea* 'Doomsday', *Dionaea* 'Cthugha', *Dionaea* 'Envy', *Dionaea* 'Lust', *Dionaea* 'CCCP Red Onyx'.

Abstract: Five new carnivorous plant cultivars are named and described: *Dionaea* 'Doomsday', *Dionaea* 'Cthugha', *Dionaea* 'Envy', *Dionaea* 'Lust', *Dionaea* 'CCCP Red Onyx'.

Dionaea 'Doomsday'

Submitted: 7 August 2020

Sown in 2013 and selected in 2015, *Dionaea* 'Doomsday' is a very chaotic plant which exhibits a high level of mutation, deformation of the plant, be it the trap, the petiole, the flower stalk or the flower itself.

No more than 6 cm tall, the petiole is slim, 4 to 8 mm wide, with a trap of 2-3 cm at best.

Traps without mutations can seldom occur in winter while being prostrate, but have yet to be seen in growth season while the plant is erect.

A slight red coloration can be seen inside the trap.

Somehow recalling *Dionaea* 'Master of Disaster', *Dionaea* 'Doomsday' has proven being much more stable in more than five years of observation, with a similar to higher level of malformation.

Depending on how much mutation there is, the traps may not be closed or triggered and the flowers can display a deformed and sterile pistil.

Doomsday, "the last day of the world's existence", inspired the cultivar name for its apocalyptical shape.

The plant must be reproduced vegetatively through rhizome or leaf cutting to preserve the cultivar characteristics.

—Teddy Vayssade • En Jacquet • 82500 FAUDOAS • France • ted02@orange.fr

Dionaea 'Envy'

Submitted: 7 August 2020

Dionaea 'Envy' was selected in 2018 from a seed sown in 2015. The plant was noticed first for its unique combination of very small teeth (as *Dionaea* 'Microdent') and its crested petiole (as *Dionaea* 'Schuppenstiel II'). I later noticed that it does not exhibit any more coloration in season, staying entirely yellow/green all year, even under strong sunlight.

The plant remains prostrate, its adult leaves have a petiole about 4 cm long and 0.6 cm wide at best and a trap about 3 to 4 cm long.

A childish dream of mine was to have a set of cultivars named after the seven deadly sins. *Dionaea* 'Envy' ('Jalousie' in French) represents jealousy, as in the sayings "being green with envy" or "jealousy is an ugly trait", which could both define the plant.

The plant must be reproduced vegetatively through rhizome or leaf cutting to preserve the cultivar characteristics.

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Dionaea 'Lust'

Submitted: 7 August 2020

Dionaea 'Lust' germinated in July 2015 from seeds of unknown parentage and was rapidly selected, in May 2016, as the plant stood out among all other seedlings. It is a fast grower, dark red / garnet with a yellow edging trap and with very long and slim leaves.

The petiole is thin (1-2 mm wide) and long (11-12 cm length) holding a normal sized trap (about 3 cm). Erect most of the year, the plant has a more prostrate period with broader leaves in winter.

It is similar to *Dionaea* 'Long Petiole', *Dionaea* 'WIP Slim Snapper' or *Dionaea* "Spider" but differs in color with a deep dark red coloration.

Named after one of the seven deadly sins, *Dionaea* 'Lust' ('Luxure' in French) is also a tribute to the mangaka Hiromu Arakawa with her Fullmetal alchemist character, Lust, who has a skill which reminds the shape and color of the cultivar.

The plant must be reproduced vegetatively through rhizome or leaf cutting to preserve the cultivar characteristics.

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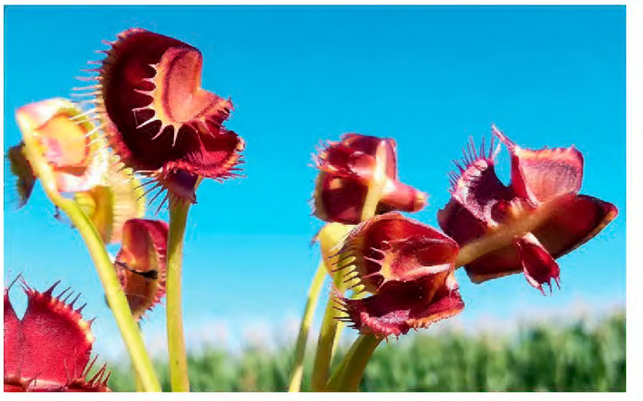
Dionaea 'Cthugha'

Submitted: 7 August 2020



This plant was selected in 2015 from a seed sown in 2013, of a cross between *Dionaea* 'Paradisia' (seed plant) and *Dionaea* 'Mirror' (pollen plant).

Defined by a very mutant and deformed trap which becomes deep red while the petiole stays green. *Dionaea* 'Cthugha' is erect in its growth season (with a petiole 8 cm long) and prostrate in winter. The deformations occur in both state, being more pronounced while being erect. The flower stalk of the plant and its flowers show random deformations too. Traps without mutation can occur but are a very rare sight. Being observed for more than five years, in other collections too, the long-term stability of the plant is now confirmed.

Cthugha is a demonic deity in the famous H.P. Lovecraft Cthulhu's myth, appearing in a Derleth's novel in 1944. Also known as "the living flame" Cthugha's shape is uncertain and chaotic, which reminds the exploded, hazardous, and horrific aspect of the plant while its red color recalls the fire entity.

The plant must be reproduced vegetatively through rhizome or leaf cutting to preserve the cultivar characteristics.

—Teddy Vayssade • En Jacquet • 82500 FAUDOAS • France • ted02@orange.fr

Dionaea 'CCCP Red Onyx'

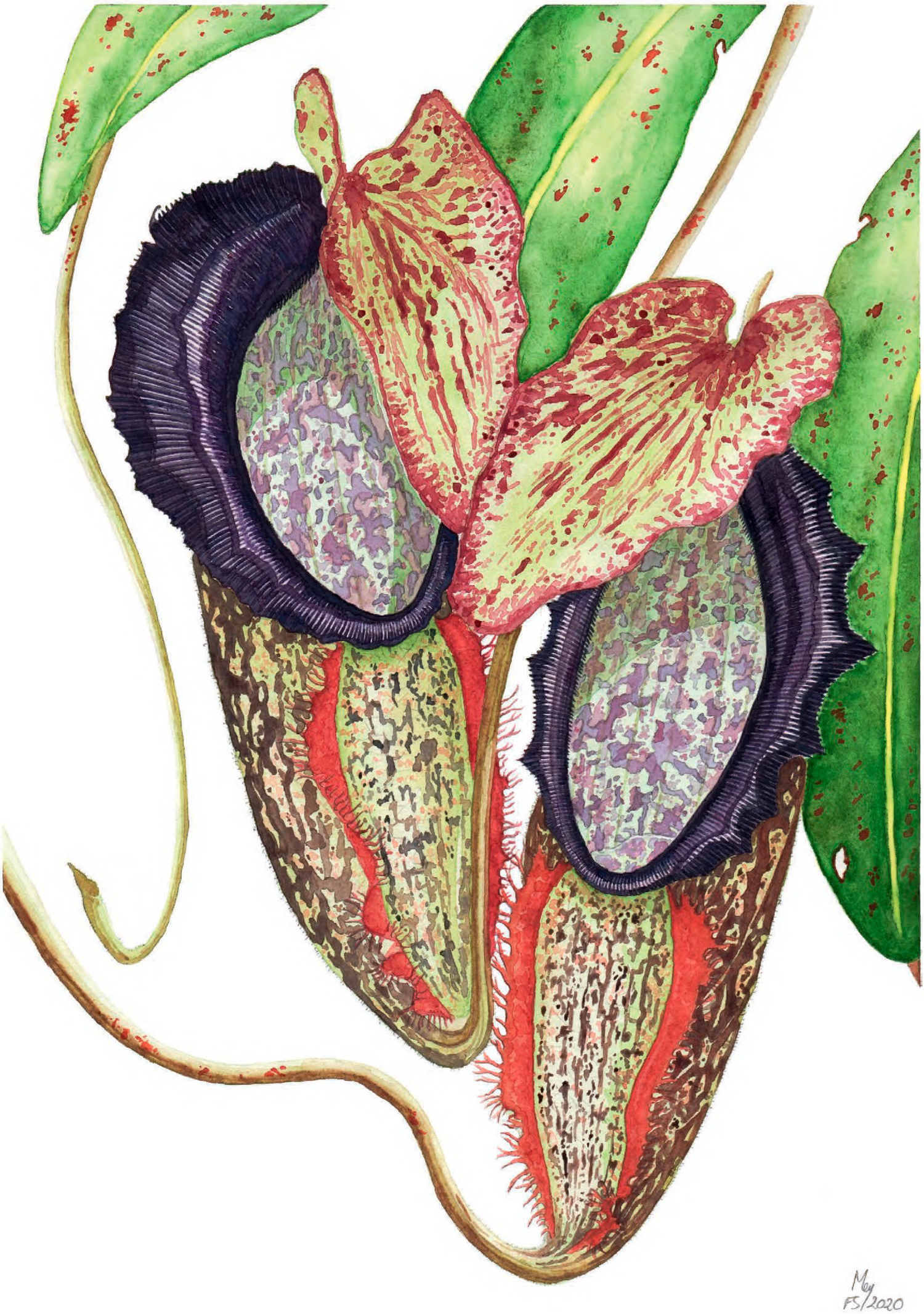
Submitted: 9 August 2020

Dionaea 'CCCP Red Onyx' was propagated by seed and selected on 31 July 2016 by Craig Heath (Crazy Craig's Carnivorous Plants). *Dionaea* 'CCCP Red Onyx' is short with standard trigger hairs, three on each side. The traps are fully functional to completely seal and digest insects. Traps are up to 1.3 cm long and up to 1 cm wide with white to red cilia. Petioles are short, up to 1.9 cm long. *Dionaea* 'CCCP Red Onyx' maintains its deep red color throughout the year with exposure to direct sunlight. There is a light band of color around the top outer trap during the early growth stages that slowly disappears with maturity. Inside trap is completely dark red without any trace of green.

The name 'Red Onyx' was suggested to me by my wife due to the deep dark red color resembling the gemstone noted for its brilliant red colors and rosette style.

Dionaea 'CCCP Red Onyx' must only be propagated vegetatively to preserve the unique characteristic of the cultivar.

—Craig Heath • Crazy Craig's Carnivorous Plants • Lorton • Virginia • USA • Craigisterh@msn.com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